

## First records of giant pill-millipedes from Laos (Diplopoda, Sphaerotheriida, Zephroniidae)

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### Abstract

Before this study, giant pill-millipedes (order Sphaerotheriida) were unknown from Laos despite their presence in all surrounding countries. As by-catch from collections by arachnologists, 31 specimens of Sphaerotheriida from Laos became available for study. The sample included 14 species. Three species were only represented by females, which are described but cannot be named. Of the remaining 11 species, a single species belongs to the genus *Zephronia* Gray, 1832: *Z. laotica* n. sp.; and the other ten belong to the genus *Sphaerobelum* Verhoeff, 1924: *S. bolavensis* n. sp., *S. phouloei* n. sp., *S. denticulatum* n. sp., *S. spinatum* n. sp., *S. lachneeis* n. sp., *S. peterjaegeri* n. sp., *S. nigrum* n. sp., *S. splendidum* n. sp., *S. laoticum* n. sp., and *S. schwendingeri* n. sp. This more than doubles the known diversity of *Sphaerobelum*. Here, I integratively describe these species, combining morphology and DNA barcodes with a molecular analysis including all Zephroniidae species deposited on GenBank—including the only giant pill-millipede species known from Cambodia, *Zephronia davydoffi* Attems, 1953. An updated determination key to the species of the genus is presented. *Zephronia laot-*

*ica* n. sp. belongs to the monophyletic *Zephronia* sensu stricto group, which is confirmed by molecular barcoding. In contrast, most species of *Sphaerobelum* are in a weakly supported clade. Genetically, *Sphaerobelum* species differ greatly from one another, with most p-distances >15%. The lowest observed p-distance (9.8%) is between *S. truncatum* Wongthamwanich *et al.* 2012 from Thailand and *S. peterjaegeri* n. sp.

**Key words:** SE Asia, biodiversity, soil arthropods, *Sphaerobelum*, *Zephronia*

## Introduction

Laos is a landlocked, tropical country that belongs to the biodiverse Great Mekong region which yielded more than 2,200 new species discoveries in the last 20 years (WWF 2016). Unfortunately, Laotian forests are currently shrinking at an alarmingly fast rate, with illegal logging and timber smuggling to Vietnam occurring on a large scale (EIA 2011; Smirnov 2015; Gan *et al.* 2016).

Millipedes, class Diplopoda, with more than 12,000 species (Enghoff *et al.* 2015) are the third most species-rich group of land arthropods on Earth and are poorly documented from Laos. As detritivores, most millipede species live in forests and are mesophilous, prone to local endemism (e.g. Wesener 2009; Car & Harvey 2014; Wesener & Conrad 2016), and therefore greatly impacted by ongoing forest destruction. The current Diplopoda checklist for Laos lists only 34 species (Likhitrakarn *et al.* 2014a), which is probably less than 10% of what can be expected. Indeed, recent taxonomic studies have already added 29 additional species (Likhitrakarn *et al.* 2014a, 2014b, 2014c, 2015a, 2015b, 2016a, 2016b; 2017; Golovatch 2016a, 2016b; Golovatch *et al.* 2016a, 2016b; Liu *et al.* 2017a). The record of Diplopoda in Laos is currently limited to species from just seven of the 16 orders. Conspicuous is the absence of any records of giant pill-millipedes, order Sphaerotheriida, that are otherwise present in all surrounding countries: Myanmar with 12 species (Likhitrakarn *et al.* 2017), China with five species (Wesener 2016a), Vietnam with 16 species (Golovatch *et al.* 2012; Semenyuk *et al.* 2018), Cambodia with one species (Likhitrakarn *et al.* 2015c), and Thailand with two species (Wongthamwanich *et al.* 2012).

Here I describe the first Sphaerotheriida species known from Laos based on the collections of three European museums.

## Material and methods

**Morphological study:** Specimens were observed under an Olympus SZX12 stereo-microscope. For scanning electron microscopy, samples were dehydrated in 100% ethanol for 12 hours, mounted on aluminum stubs, air-dried for 12 hrs at 45°C and sputter coated with a 50 nm layer of pure gold in a Hummer VI sputtering system (Anatech LTD, USA). Samples were observed and imaged with a Supra VR 300VP SEM (Carl Zeiss AG, Oberkochen, Germany). Photographs were taken at multiple focal planes with a DUN (Palmyra, Virginia) BK-Plus imaging-system based at the ZFMK. Images were stacked using the software Auto-Montage (Syncroscopy). Images were then modified using Adobe Photoshop version CS2 and assembled into plates using Adobe Illustrator version CS2. Naming of morphological structures follows the literature (Wesener & Sierwald 2005; Wesener 2016a, 2016b).

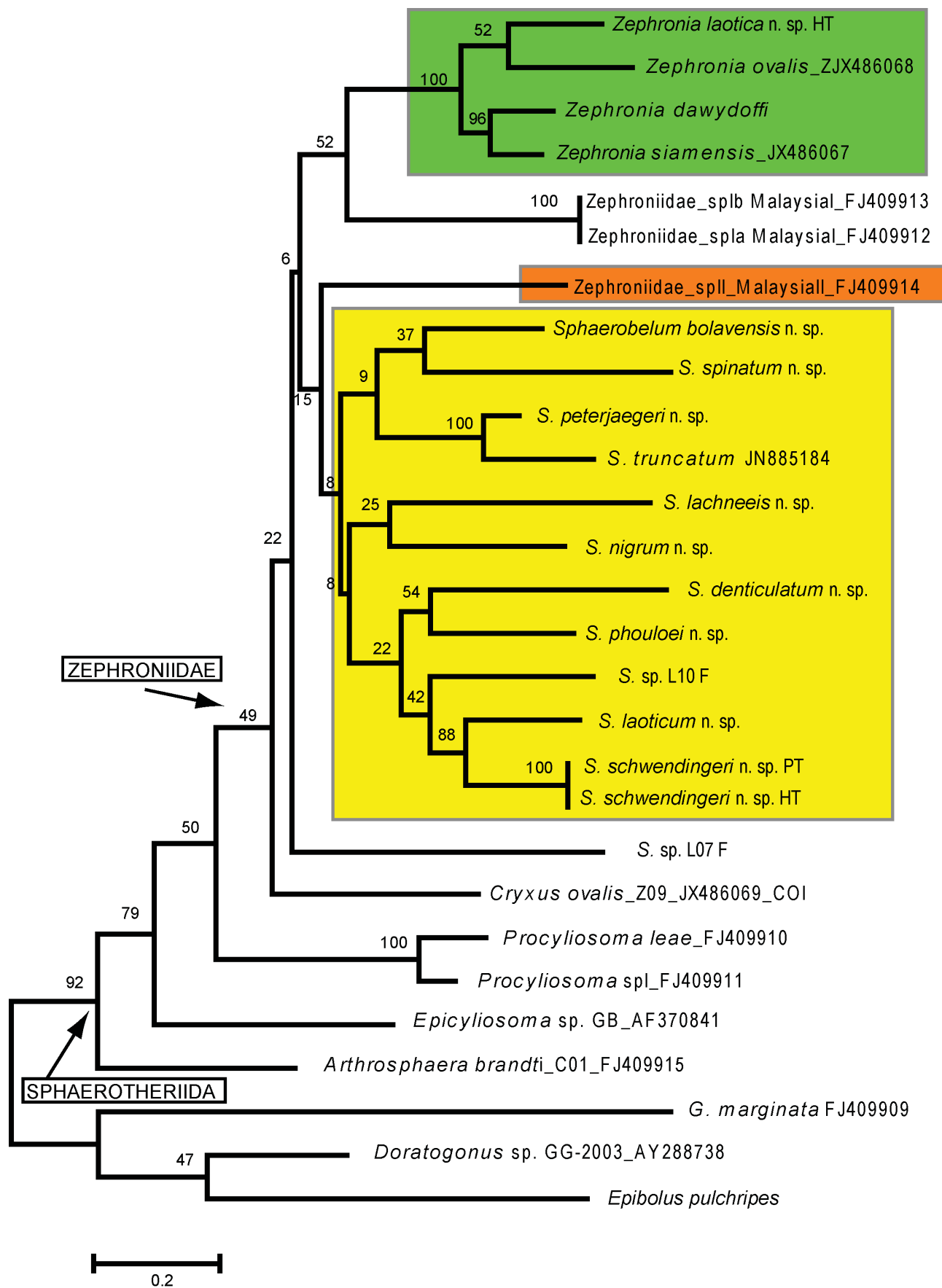
**DNA extraction, amplification and sequencing:** The DNA extraction, amplification, and sequencing protocol was similar to that employed in earlier studies (Sagorny & Wesener 2017; Wesener 2015; 2018), utilizing the degenerate primer pair HCO-JJ/LCO-JJ (HCOJJ AWA CTT CVG GRT GVC CAA ARA ATC A/ LCOJJ CHA CWA AYC ATA AAG ATA TYG G) (Astrin & Stüben 2008). The 11 new sequences have been uploaded to GenBank under the accession codes: MK330970–MK330984 (Table 1).

**Alignment and Molecular Analysis:** Sequences were aligned by hand in Bioedit (Hall 1999). The final aligned dataset included 28 nucleotide sequences with 657 positions (15 newly sequenced and 13 from GenBank, see Table 1). Phylogenetic analyses were conducted in MEGA6 (Tamura *et al.* 2013). A likelihood ratio model test, as implemented in MEGA6 (Tamura *et al.* 2013), was conducted to find the best-fit maximum likelihood nucleotide substitution model. Models with the lowest BIC scores (Bayesian Information Criterion) were considered to describe the best-fit substitution scheme. All codon positions were included: 1st+2nd+3rd. The model test selected the General-Time-Reversible (GTR) model (Nei & Kumar 2000) with gamma distribution and invariant sites as the best-fit model (lnL -8204.58, Gamma 0.298, R: 4.2, Freq A: 0.273, T: 0.336, C: 0.228, G: 0.162).

The evolutionary history was inferred with MEGA6 by using a maximum likelihood method based on the GTR model (Nei & Kumar 2000). The tree with the highest log likelihood (-8204.82) is shown in Figure 1. A bootstrap analysis was conducted with 1000 pseudoreplicates (Felsenstein 1985). The percentage of nodes among 1000 bootstrap pseudoreplicates in which the associated taxa occurred together is shown next to the branches. A start tree for the heuristic search was obtained by neighbor-joining using the BioNJ algorithm applied to a matrix of pairwise distances estimated using the maximum composite likelihood (MCL) approach. The topology with the maximum log likelihood value was then retained (Fig. 1). A discrete gamma distribution was used to model evolutionary rate differences among sites (5 categories (+G, parameter = 0.3047)). The rate invariant model allowed for some sites to be evolutionarily invariable ([+I], 19.7304% sites). The tree (Fig. 1) is drawn to scale, with branch lengths proportional to the number of expected substitutions per site (Fig. 1, scale bar). The number of uncorrected pairwise DNA base differences per site were calculated in MEGA6 (Tamura *et al.* 2013). In the distance analysis, all positions containing 'N's were omitted for each sequenced pair.

**TABLE 1.** Analysed specimens, voucher and GenBank number. Specimens marked by an \* have been newly sequenced. Abbreviations: **QVMAG** = Queen Victoria Museum and Art Gallery, Tasmania, Australia; **MHNG** = Muséum d'histoire naturelle de la ville de Genève, Geneva, Switzerland; **SMF** = Senckenberg Museum Frankfurt, Germany; **ZFMK** = Zoological Research Museum Koenig, Bonn, Germany; **ZMUC** = Zoologisk Museum, University of Copenhagen, Denmark.

Species	Voucher #	GenBank #
Spirostreptida, <i>Doratogonus</i> sp. GG-2003	unknown	AY288738
Spirobolida, <i>Epibolus pulchripes</i> *	ZFMK MyrXX	MK330970
Glomerida, <i>Glomeris marginata</i>	ZFMK Myr009	FJ409909
Sphaerotheriida, unknown family, <i>Epicyllosoma</i> sp. GB	unknown	AF370841
Sphaerotheriida, Procyliosomatidae, <i>Procyliosoma leae</i>	QVMAG 23:45801	FJ409910
Sphaerotheriida, Procyliosomatidae, <i>Procyliosoma</i> sp.	QVMAG 23:25721	FJ409911
Sphaerotheriida, Arthrosphaeridae, <i>Arthrosphaera brandti</i>	FMNH-INS 8650	FJ409915
Sphaerotheriida, Zephroniidae sp. Ia	ZFMK Myr014	FJ409912
Sphaerotheriida, Zephroniidae sp. Ib	ZFMK Myr015	FJ409913
Sphaerotheriida, Zephroniidae sp. II (unknown genus)	lost	FJ409914
Sphaerotheriida, Zephroniidae, <i>Sphaerobelum truncatum</i>	FMNH-INS 72673	JN885184
Sphaerotheriida, Zephroniidae, <i>Zephronia siamensis</i>	FMNH-INS-72669	JX486067
Sphaerotheriida, Zephroniidae, <i>Zephronia ovalis</i>	ZFMK Myr0832	JX486068
Sphaerotheriida, Zephroniidae, <i>Cryxus ovalis</i>	ZFMK Myr0824	JX486069
Sphaerotheriida, Zephroniidae, <i>Zephronia dawydoffi</i> *	ZFMK Myr4504	MK330971
Sphaerotheriida, Zephroniidae, <i>Zephronia laotica</i> n. sp. *	ZFMK Myr3502	MK330977
Sphaerotheriida, <i>Sphaerobelum bolavensis</i> n. sp. *	MHNG LT-10/24	MK330982
Sphaerotheriida, <i>Sphaerobelum phouloei</i> n. sp. *	ZMUC00040257	MK330974
Sphaerotheriida, <i>Sphaerobelum denticulatum</i> n. sp. *	MHNG LT-10/12	MK330983
Sphaerotheriida, <i>Sphaerobelum spinatum</i> n. sp. *	ZMUC00040258	MK330973
Sphaerotheriida, <i>Sphaerobelum lachneeis</i> n. sp. *	MHNG LT-10/12	MK330982
Sphaerotheriida, <i>Sphaerobelum peterjaegeri</i> n. sp. *	SMF SD553	MK330972
Sphaerotheriida, <i>Sphaerobelum nigrum</i> n. sp. *	SMF	MK330976
Sphaerotheriida, <i>Sphaerobelum laoticum</i> n. sp. *	SMF	MK330975
Sphaerotheriida <i>Sphaerobelum schwendingeri</i> n. sp. *	MHNG LT 10/03	MK330978
Sphaerotheriida <i>Sphaerobelum schwendingeri</i> n. sp. *	SMF	MK330981
Sphaerotheriida, <i>Sphaerobelum</i> sp. L07 *	ZMUC00040261	MK330979
Sphaerotheriida, <i>Sphaerobelum</i> sp. L10*	SMF	MK330980



**FIGURE 1.** Maximum likelihood tree obtained from the COI dataset under the GTR+I+G model with bootstrap support values (1,000 pseudoreplicates). Colours used to separate genera. Green = *Zephronia* sensu stricto; Yellow = *Sphaerobelum*.



## Museum acronyms:

**MHNG** = Muséum d'histoire naturelle de la ville de Genève, Geneva, Switzerland;

**SMF** = Senckenberg Museum Frankfurt, Germany;

**ZFMK** = Zoological Research Museum Koenig, Bonn, Germany;

**ZMUC** = Zoologisk Museum, University of Copenhagen, Denmark.

## Results

**Tree description and genetic distances between species:** While the gene tree may not be suitable to reconstruct deep phylogenies, the order Sphaerotheriida and the family Zephroniidae are recovered as monophyletic (Fig. 1). The genus *Cryxus* Leach, 1814 is sister to the remaining species of Zephroniidae, followed by a shallow grouping uniting most species of *Sphaerobelum*, with the exception of *Sphaerobelum* sp. L07 (a single female specimen). Within *Sphaerobelum*, two clades have high bootstrap support: the clade uniting *S. truncatum* Wongthamwanich *et al.*, 2012 from Thailand with *S. peterjaegeri* **n. sp.**; and the group uniting *S. laoticum* **n. sp.** with *S. schwendingeri* **n. sp.** (Fig. 1, highlighted in yellow). *Zephronia* sensu stricto (Semenyuk *et al.* 2018) is a well-supported group with 100% bootstrap support (Fig. 1, highlighted in green). Both *Z. dawydoffi* Attems, 1953 from Cambodia and *Z. laotica* **n. sp.** occur within this clade: *Z. laotica* **n. sp.** sister with *Z. ovalis* from Vietnam and *Z. dawydoffi* in a well-supported sister group with *Z. siamensis* from Thailand (Fig. 1).

The close relationship of *Z. dawydoffi* and *Z. siamensis* is reflected by the distance analysis and both species differ by 9.6%, the lowest p-distance between two Zephroniidae species. The genetic distance between the morphologically similar *Sphaerobelum truncatum* and *S. peterjaegeri* is similarly low at 9.8 %. Most other genetic distances between the analyzed species of the genus *Sphaerobelum* are >15%, and among the Zephroniidae commonly between 18–23 %.

## Taxonomy

### Class Diplopoda de Blainville in Gervais, 1844

### Order Sphaerotheriida Brandt, 1833

### Family Zephroniidae Gray, 1843

### Genus *Zephronia* Gray, 1832

Type species: *Zephronia ovalis* Gray, 1832.

Other taxa included: 41 (Wesener 2016a; Semenyuk *et al.* 2018).

**Distribution:** Mainly NE India, Nepal and Myanmar, a handful of species also in SE Asia.

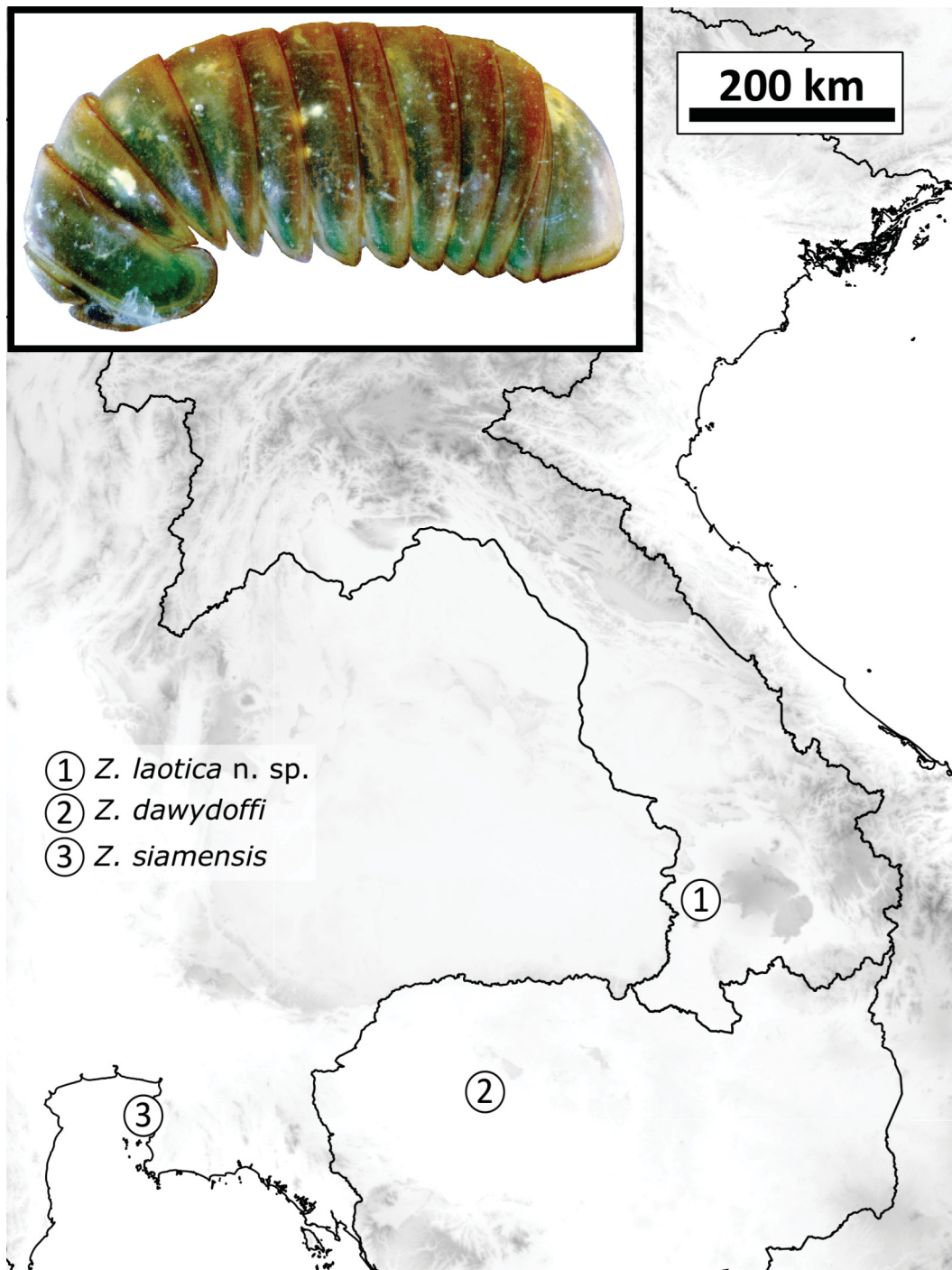
### *Zephronia laotica* new species

Figures 2–4.

**Material examined:** Type specimens. 1 M holotype (ZFMK MYR3502) from Laos, Champasak Province, east of Mekong, Garden of Erawan Riverside Hotel (N 15°6'27.0", E 105°49'14.3"), leg. Siegfried Huber, 10–15.xi.2012. 1 F paratype (ZFMK MYR8098), same data as holotype.

**Diagnosis.** *Zephronia laotica* **n. sp.** belongs to the *Zephronia* sensu stricto group based on the position of the organ of Tömösváry, located next to the aberrant ocelli, not inside the antennal groove (Semenyuk *et al.* 2018). *Zephronia* sensu stricto encompasses: *Z. ovalis* Gray, 1832; *Z. konkakinhensis* Semenyuk *et al.*, 2018; *Z. montis* Semenyuk *et al.* 2018 from Vietnam; *Z. siamensis* Hirst, 1907, the only species of the genus known from Thailand;

and *Z. dawydoffi* Attems, 1953, the only giant pill-millipede species known from Cambodia. *Zephronia laotica* **n. sp.** differs from *Z. konkakinhensis* and *Z. montis* in the walking legs that lack strong teeth on the femur, and *Z. ovalis* which has weak teeth at the mesal margin of the femur (Fig. 3B). *Zephronia laotica* **n. sp.** differs from *Z. ovalis*, *Z. siamensis* and *Z. dawydoffi* also in the differently shaped telopoditomers 3 and 4 of the anterior telopods, the elongation of telopoditomere 3 and the small size of telopoditomere 4 are unique (Figs 4B–D), a different bright green colour of the tergites (Fig. 2A), leg 3 lacking an apical spine, and the presence of two locking carinae on each side of the anal shield.



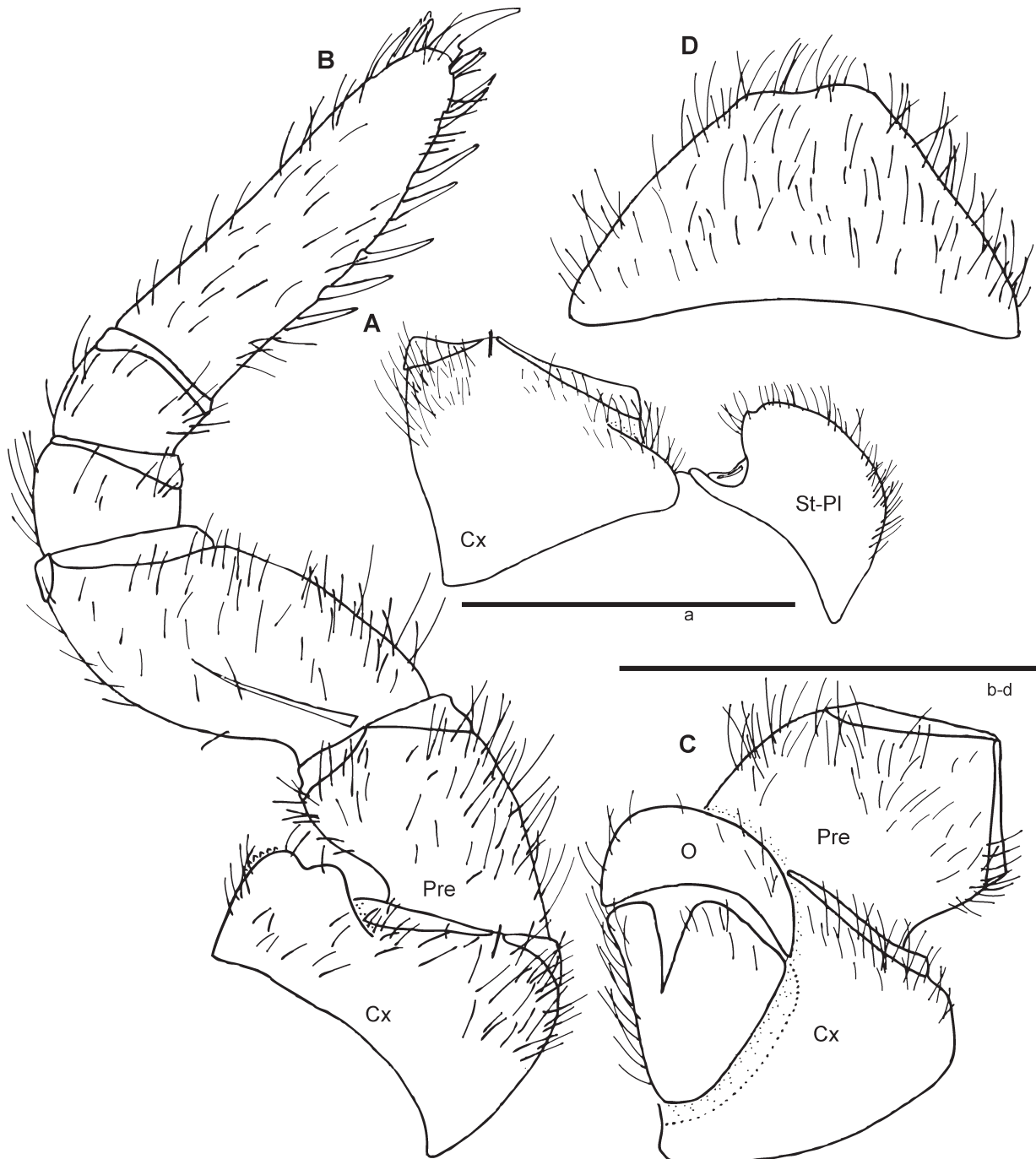
**FIGURE 2.** Distribution map and habitus photograph of *Zephronia* species, *Z. laotica* **n. sp.**

**Description.** Based on holotype male and paratype female.

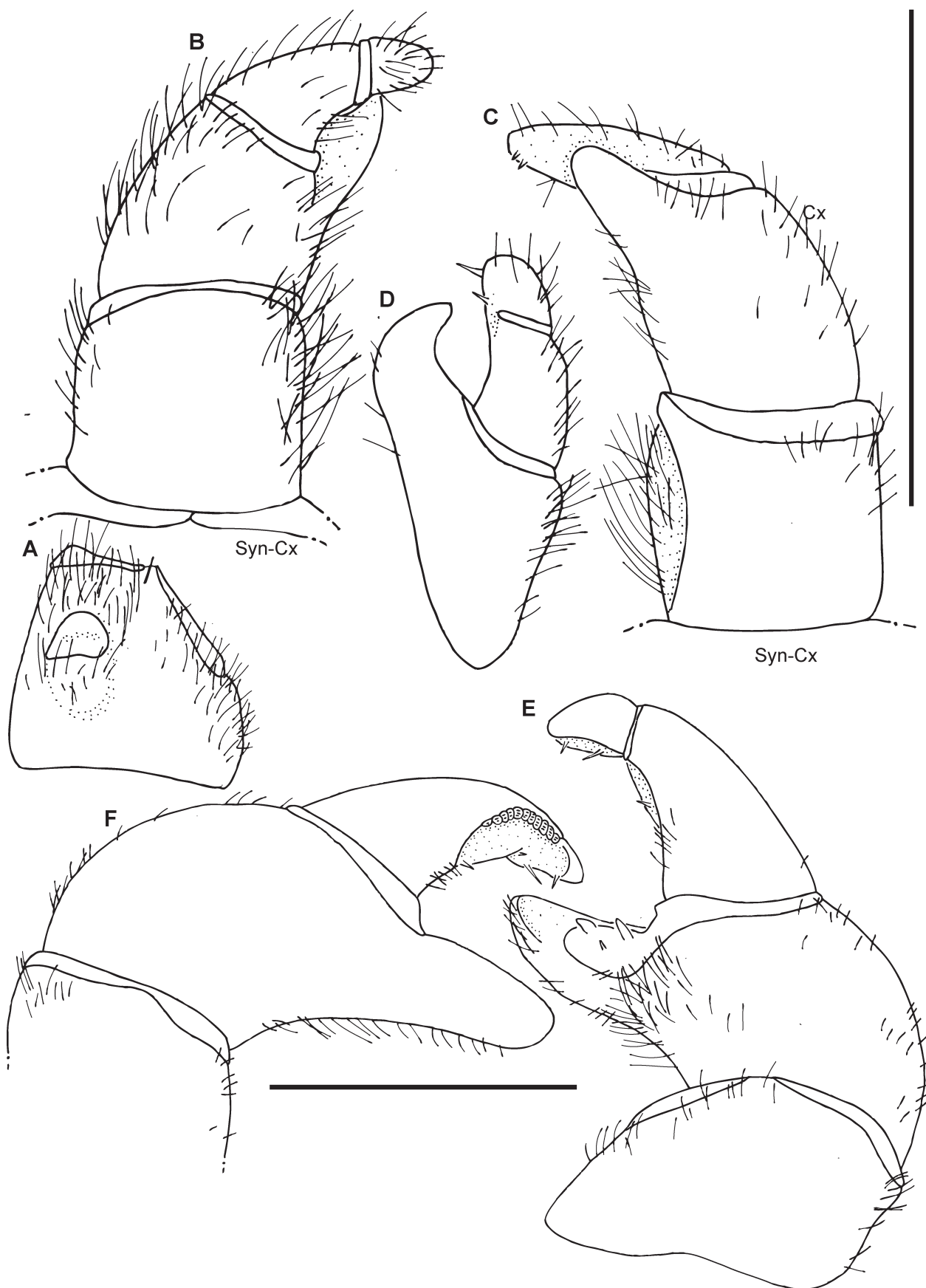
**Measurements:** Holotype male. Body length = 15.6 mm. Width, of thoracic shield = 6.7 mm, of tergite 7 = 7.2 mm (= broadest). Height, of thoracic shield = 4.2 mm, of tergite 7 = 4.3 mm (= highest). Female: body length = ca

14.1 mm. Width, of thoracic shield = 6.1 mm, of tergite 7 = 6.9 mm (= broadest). Height, of thoracic shield = 3.8 mm, of tergite 7 = 4.2 mm (= highest). **Coloration:** in preserved specimens, head and collum green. Tergites bright green, posterior half light brown. Antennae and legs green (Fig. 2A).

**Head:** wide and short. Eyes with >75 ocelli. Aberrant ocellus located inside antennal groove. Antennae short, with rounded joints, extending posteriorly to leg-pair 3. Sizes of antennomeres 1=2=3=4=5<<6. Antennomere 6 densely pubescent, with a few sensilla basiconica surrounding apical disc. Shape sexually dimorphic: in female cylindrical, in male laterally flattened, axe-shaped. Male apical disc with 61/65 apical sensory cones, that of female with 32/34 apical cones. Organ of Tömösváry located at a projected brim close to the ocelli at margin of antennal groove. **Gnathochilarium:** structure typical of the order. Sensory cones of palpi all located in single field. **Mandibles** not examined.



**FIGURE 3.** *Zephronia laotica* n. sp., **A, B:** male holotype (ZFMK MYR3502); **C, D:** female paratype (ZFMK MYR8098); **A:** coxa of first left leg with first stigmatic plate; **B:** 9th right leg; **C:** coxa and prefemur of second left leg with vulva; **D:** subanal plate. Abbreviations: **Cx** = coxa; **O** = operculum of vulva; **Pre** = prefemur; **St-Pl** = stigmatic plate. Scale bars = 1 mm.



**FIGURE 4.** *Zephronia laotica* n. sp., male holotype (ZFMK MYR3502); **A:** coxa of second left leg with gonopore; **B:** left anterior telopod, anterior view; **C:** left anterior telopod, posterior view; **D:** left anterior telopod, lateral view; **E:** right posterior telopod, anterior view; **F:** right posterior telopod, posterior view. Abbreviations: **Syn-Cx** = syncoxite. Scale bars = 1 mm.



**Stigmatic plates:** first stigmatic plate triangular, apex broadly rounded, slightly curved towards coxa 1 (Fig. 3A). **Laterotergites:** first laterotergite tip weakly extended, pointed process. Second laterotergite with even shorter process, well-rounded apex. **Collum:** glabrous, except for margins which have a few isolated and long setae. **Thoracic shield:** surface as in tergites. Shallow grooves filled with numerous long setae, no keels. **Tergites:** surface shiny, glabrous, weakly coriaceous. Tips of paratergites of midbody tergites straight (Fig. 2A). **Endotergum:** inner section with few longer setae. Middle area with a single row of dense round, shallow, cuticular impressions; distance between impressions slightly smaller than their diameter. Apically, 1–2 dense rows of short marginal bristles, the longest just protruding above tergal margin. Bristles not smooth, but with numerous small spicules. **Anal shield:** slightly sexually dimorphic, in female large and well-rounded, in male more rectangular, in both sexes glabrous. Surface similar to that of tergites. Underside with two locking carinae; first short, as long as those of tergites, second as long as first, but much weaker. **Legs:** leg-pair 1 with 1 or 2 ventral spines, leg-pair 2 with 4, leg-pair 3 with 6. First three leg-pairs without an apical spine. Leg-pairs 4–21 with 7–9 ventral spines and 3–5 apical spines. In leg-pair 9, femur 1.5 times, tarsus 3.5 times longer than wide (Fig. 3B). All podomeres setose. Coxa with a large, well-rounded process. Coxal process absent on leg-pair 1 (Fig. 3A) and 2 (Figs 3C, 4A).

**Female sexual characters:** vulva small, covering 1/2 of coxa, located at mesal margin, extending mesally to basal third of prefemur length (Fig. 3C). Operculum rounded. **Subanal plate:** large, tall, triangular, with a well-rounded tip (Fig. 3D).

**Male sexual characters:** gonopore covered with a single, undivided, triangular, sclerotized plate (Fig. 4A). **Anterior telopods** (Figs 4B–D): first telopoditomere rectangular, slightly longer than wide. Telopoditomere 2 large, as long as telopoditomes 3 and 4 combined. Process of telopoditomere 2 located posteriorly, but partly visible laterally in anterior view. Process of telopoditomere 2 wide, broader than telopoditomes 3 and 4. Process of telopoditomere 2 wide, visible mesally in anterior view. Process of telopoditomere 2 tapering apically, well-rounded, protruding as high as basal part of telopoditomere 4. Telopoditomere 3 slender, 1.5 longer than wide, twice as long as telopoditomere 4. Telopoditomere 4 very short, in posterior aspect without any teeth, but with two prominent spines. All podomeres covered with long sparse setae, except for central part of telopoditomere 1 and posterior surfaces of 3 and 4. **Posterior telopods** (Figs 4E, F): first telopoditomere stout and narrow, twice as wide as long. Immobile finger (process of telopoditomere 2) as long as movable finger and consisting of telopoditomes 3 and 4. Immobile finger wide, 1.9X longer than wide, weakly tapering apically, not curved. Margin towards movable finger genus-characteristic: with two large, triangular, membranous lobes, a spine, and several rows of circular sclerotized spots. Telopoditomere 3 elongated, typical of the genus: twice as long as telopoditomere 4. Margin near immobile finger with a large membranous lobe and a single long and slender spine, posterior surface with a row of 11 crenulate and sclerotized teeth. Telopoditomere 4 slender, only 2/3 as wide as telopoditomere 3, 2X longer than wide, slightly tapering apically. Telopoditomere 4 with at inner margin two long spines and a single membranous lobe. Entire telopod with few setae, mostly at margins at on anterior side of telopoditomere 2.

**Derivatio nominis:** laotica, noun in apposition, after Laos, as this is the first *Zephronia* known from this country.

## Genus *Sphaerobelum* Verhoeff, 1924

Type species: *Sphaerobelum clavigerum* Verhoeff, 1924, from Vietnam

Other taxa included (15):

*S. hirsutum* Verhoeff, 1924 (Vietnam)

*S. bicornis* Attems, 1938 (Vietnam)

*S. separatum* Attems, 1953 (Vietnam)

*S. truncatum* Wongthamwanich, 2012 (Thailand)

*S. cattense* Semenyuk, Golovatch & Wesener, 2018 (Vietnam)

*S. konkakhinhense* Semenyuk, Golovatch & Wesener, 2018 (Vietnam)

*S. bolavensis* sp. nov. (Laos)

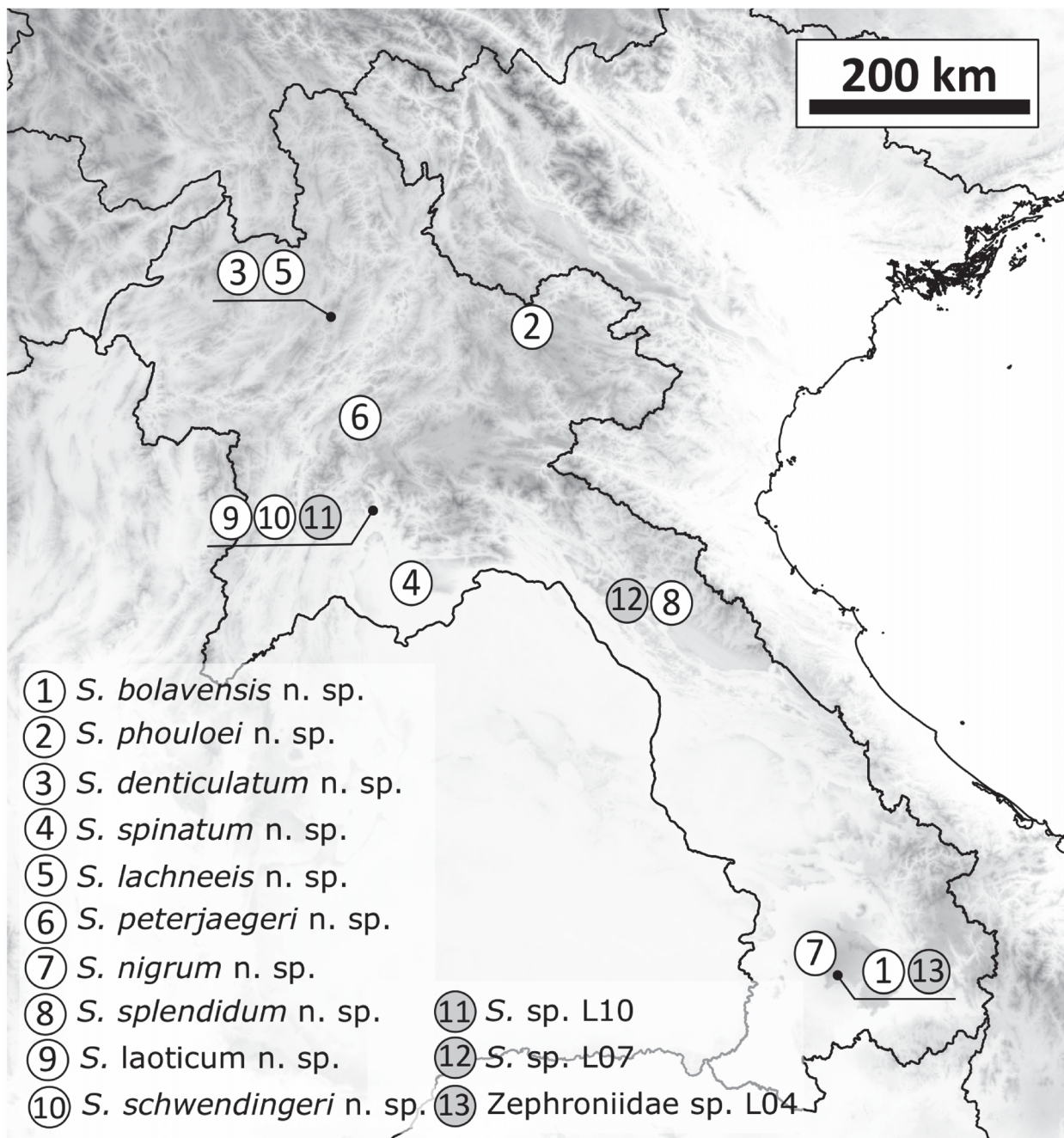
*S. phoulouei* sp. nov. (Laos)



*S. denticulatum* **sp. nov.** (Laos)  
*S. spinatum* **sp. nov.** (Laos)  
*S. lachneeis* **sp. nov.** (Laos)  
*S. peterjaegeri* **sp. nov.** (Laos)  
*S. nigrum* **sp. nov.** (Laos)  
*S. splendidum* **sp. nov.** (Laos)  
*S. laoticum* **sp. nov.** (Laos)  
*S. schwendingeri* **sp. nov.** (Laos)

**Distribution:** Vietnam, with a single species (*S. truncatum*) known from northern Thailand and ten new species described here from Laos (Fig. 5).

**Remarks:** For a recent revision of the generic characters of *Sphaerobelum*, see the literature (Wesener 2016a; Semenyuk *et al.* 2018).



**FIGURE 5.** Distribution map of *Sphaerobelum* species, including the unnamed females.

## Key to species of *Sphaerobelum* (based mainly on male characters):

1. Femur of legs at mesal margin extended, with teeth (Fig. 13A). Apical margin of prefemur modified, extended into a process . . . . . 2
  - Femur of legs not extended, well-rounded (Fig. 17B). Prefemur unmodified. . . . . 9
2. Teeth on femur only at apex: 4–6 (Fig. 8A). Anterior telopod consisting of 3 podomeres . . . . . 3
  - Teeth on whole mesal margin of femur: >10. Anterior telopod always consisting of 4 telopoditomers. . . . . 4
3. Female vulval operculum strongly projecting in two processes. Posterior telopod with telopoditome 4 tip curved towards immovable finger like a small hook. . . . . *S. bicornis* Attems, 1938
  - Female vulva projecting in a mesal process (Fig. 8B). Posterior telopod: telopoditome 4 straight, not hooked (Fig. 10E). . . . . *S. bolavensis* n. sp.
4. Posterior telopod: telopoditome 4 apex weakly curved towards and overlapping immovable finger. Anterior side of immovable finger with sclerotized spots opposite to tip of telopoditome 4 (Fig. 12E). Immovable finger in anterior view with a large sclerotized spine . . . . . 5
  - Posterior telopod: telopoditome 4 straight, not curved. No sclerotized spots or a spine at immovable finger (Fig. 16E) . . . . . 6
5. Male antennae with 30–35 apical cones. Tergites covered with short setae. Legs orange. Prefemur mesal margin rounded (Fig. 11B). . . . . *S. phouloei* n. sp.
  - Male antennae with 65–70 apical cones. Tergites glabrous. Legs light brown. Prefemur mesal margin with indentations like the femur (Fig. 13A). . . . . *S. denticulatum* n. sp.
6. Male antennae red or brown, with >70 apical cones. Tergites matte. First laterotergite weakly projecting posterior-laterally. . . . . 7
  - Male antennae yellow, with 50–55 apical cones. Tergites shiny, with setae. First laterotergite strongly projecting posterior-laterally . . . . . *S. spinatum* n. sp.
7. Tergites glabrous, matte. Endotergum bristles only protruding slightly midway towards margin. Anterior telopod: telopoditomers 3 and 4 not well-separated in posterior view (Figs 21 B–D). . . . . *S. nigrum* n. sp.
  - Tergites hairy, with pits. Endotergum bristles long, protruding above tergite margin. Anterior telopod: telopoditomers 3 and 4 well separated . . . . . 8
8. Colour dark olive, posterior tergal margins with a broad, light-brown band, antennae and legs conspicuously orange. Prefemur without lateral projection. Apical margins of vulval operculum equally converging towards a mesal tip. Tip of laterotergite 1 slightly extended, well-rounded. Male antennomere 6 thickened. . . . . *S. cattense* Semenyuk *et al.*, 2018
  - Colour dark chestnut brown, posterior tergal margins black, legs dark brown, tips light brown. Lateral margin of prefemur with a sharp projection juxtaposed to coxal process. Apical margin of vulval operculum recessed centrally. Tip of laterotergite 1 slightly extended, sharp. Male antennomere 6 axe-shaped. . . . . *S. konkakinhense* Semenyuk *et al.*, 2018
9. Posterior telopod without 'hook' . . . . . 10
  - Posterior telopod: telopoditome 4 apically always with a short recurved 'hook' (Fig. 21E). . . . . 13
10. Tergites covered with very long setae. Setae longer than width of tergites (Fig. 6E). Immovable finger of posterior telopod with very long mesal extension (Fig. 18C). Antennae green. Anterior telopod suture between telopoditomers 3 and 4 weak, not visible in anterior view (Figs 18A, B). . . . . *S. lachneis* n. sp.
  - Tergites covered with short setae. Immovable finger of posterior telopod swollen, but not with such a long lateral extension. Anterior telopod: telopoditomers 3 and 4 well separated. . . . . 11
11. Podomere 3 of anterior telopod distally with a lateral extension. Posterior telopod: telopoditome 4 distally with an incurved process overlapping with process of podomere 2. Marginal setae of terga not reaching posterior margin. Tergite posterior margin well-rounded, not tessellated . . . . . *S. separatum* Attems, 1953
  - Podomere 3 of anterior telopod cylindrical, without lateral extension. Posterior telopod: telopoditome 4 without incurved process, but with 3 separate spines. Marginal setae of terga reaching posterior margin. Tergite posterior margin tessellated . . . . . 12
12. Antennae with >80 apical cones. Legs: femur 2x longer than wide. Tarsi with 7 or 8 ventral spines. Antennae and legs yellow. Vulval operculum well-rounded, not extending. . . . . *S. truncatum* Wongthamwanich *et al.*, 2012
  - Antennae with <70 apical cones. Legs: femur 1.7 times longer than wide. Tarsi with 7–10 ventral spines. Antennae and legs orange-red. . . . . *S. peterjaegeri* n. sp.
13. Tergites glabrous, at least posterior 2/3 of each tergite. . . . . 14
  - Tergites covered with short setae. Dirty olive-brown. Head punctured and densely hirsute. . . . . *S. hirsutum* Verhoeff, 1924
14. Anal shield with a short, or completely reduced locking carina. Posterior telopod: immovable finger, swollen at inner and mesal margin. Telopoditome 4 at mid-point strongly curved and overlapping immovable finger (Fig. 22G) . . . . . 15
  - Anal shield with long locking carina, >3X length of tergite carina. Posterior telopod: immovable finger, swollen only at inner margin; mesal margin straight. . . . . *S. clavigerum* Verhoeff, 1924
15. Anterior telopod: telopoditomers 3 and 4 clearly separated (Figs 21B–D). Antennae and legs brown . . . . . *S. splendidum* n. sp.
  - Anterior telopod: telopoditomers 3 and 4 separation only partly visible in anterior view (Fig. 22D). Antennae and legs red . . . . . 16
16. Process of telopoditome 2 projecting as high as basal 1/3 of telopoditome 3+4 (Fig. 22F). Anal shield with a single short locking carinae. Palpi of gnathochilarium, sensory cones located in single field. . . . . *S. laoticum* n. sp.
  - Process of telopoditome 2 projecting as high as basal 3/4 of telopoditome 3+4 (Fig. 25E). Anal shield without locking carinae. Palpi of gnathochilarium, sensory cones located in several clusters . . . . . *S. schwendingeri* n. sp.



### *Sphaerobelum bolavensis* new species

Figures 6A, 7, 8, 9A, 10.

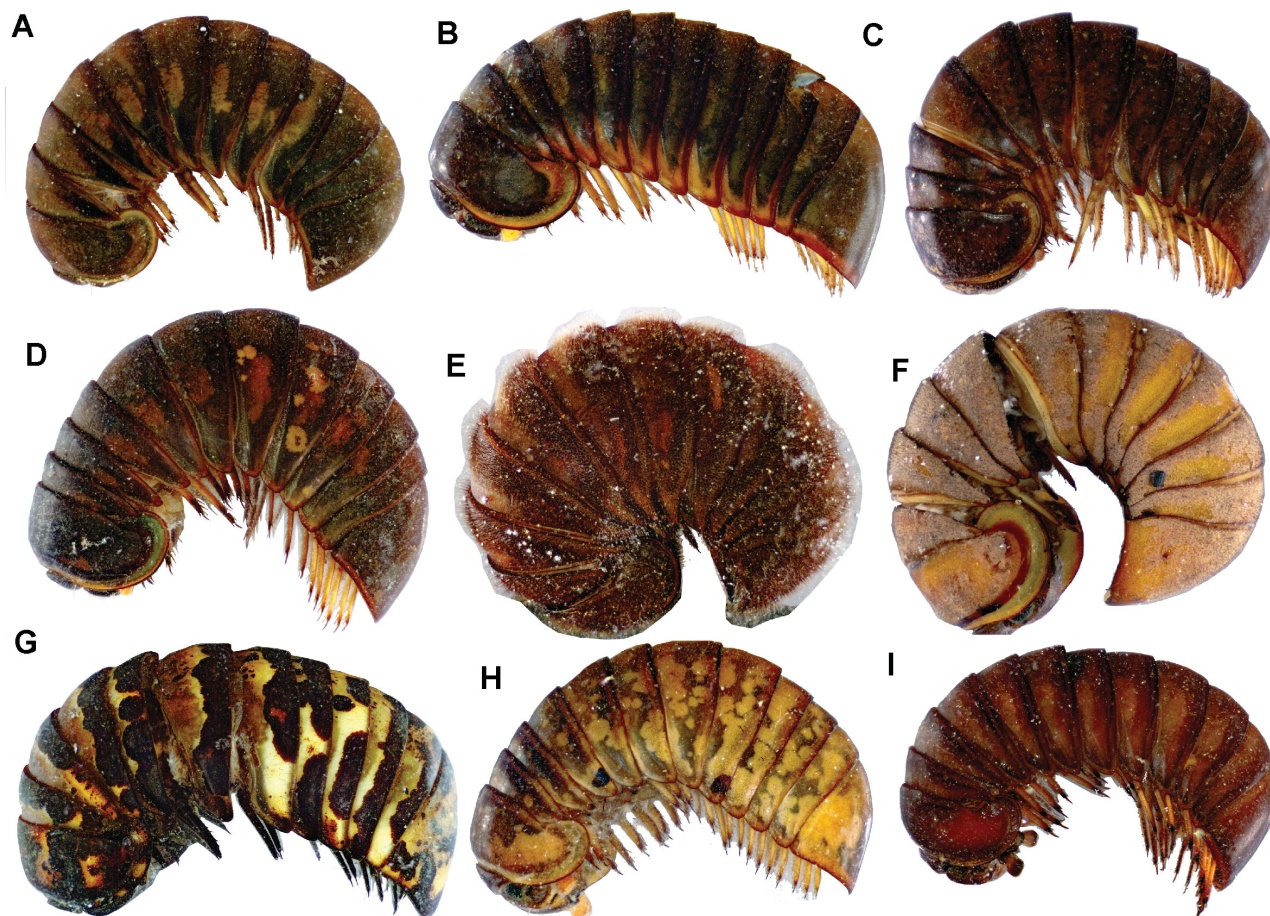
**Material examined:** Type specimens. 1 M holotype (ZMUC00040256) from Laos, Champasak Province, Bolaven Plateau, Ban Houayteuay, 1200 m (N 15°4.655', E 106°16.848') disturbed montane forest, leg. 10.XII.2007, by hand, S. Tarasov. 1 F paratype (ZFMK MYR8100), same data as holotype.

**Non-type material:** 1 F (MHNG LT-10/24) from Laos, Champasak Province, Bolaven Plateau, 3 km S of Ban Nong Luang, Tad Kameud, 1270 m (N 15°04'23", 106°12'36" E), undisturbed evergreen hill forest, 1.X.2010, leg. P. Schwendinger.

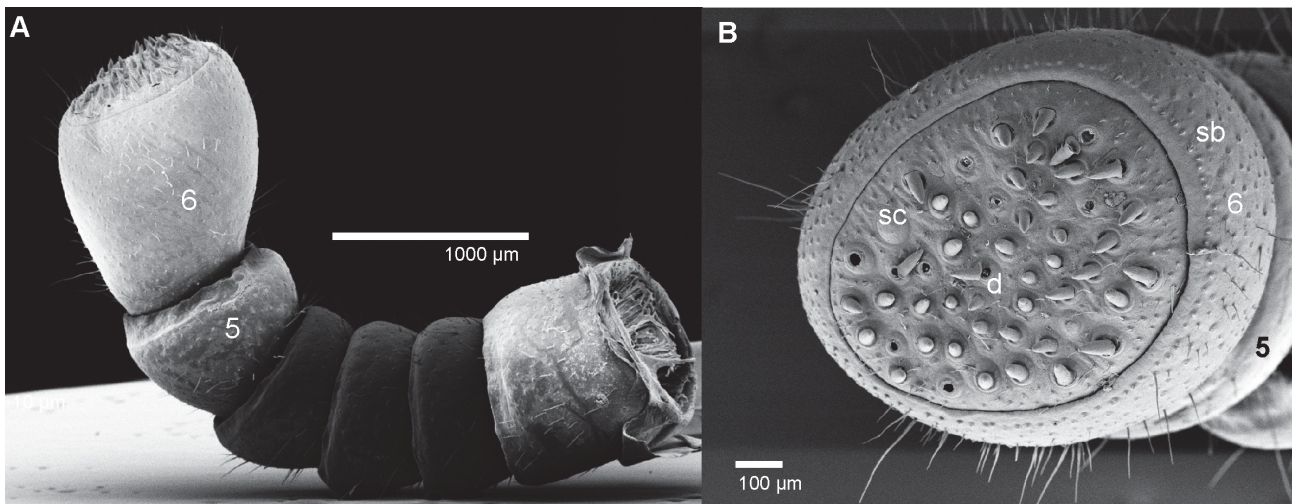
**Diagnosis:** *S. bolavensis* **n. sp.** belongs to a group of *Sphaerobelum* species in which the mesal margin of the femur is extended and apically tipped with several teeth (Fig. 8A). *Sphaerobelum bolavensis* **n. sp.** and *S. bicornis* from Vietnam are the only species with an extension only in the apical part of the femur. *Sphaerobelum bolavensis* **n. sp.** possesses a female vulval operculum only projecting in a single mesal process (Fig. 8B); in contrast, *S. bicornis* has two processes. *Sphaerobelum bolavensis* **n. sp.** has a telopoditomere 4 of the posterior telopod straight, apically without a recessed hook (Figs 10E, F); in contrast *S. bicornis* possesses a hook. *Sphaerobelum bolavensis* **n. sp.** has a short locking carina on the anal shield; whereas the carina is long in *S. bicornis*.

**Description.** Based on holotype male and paratype female.

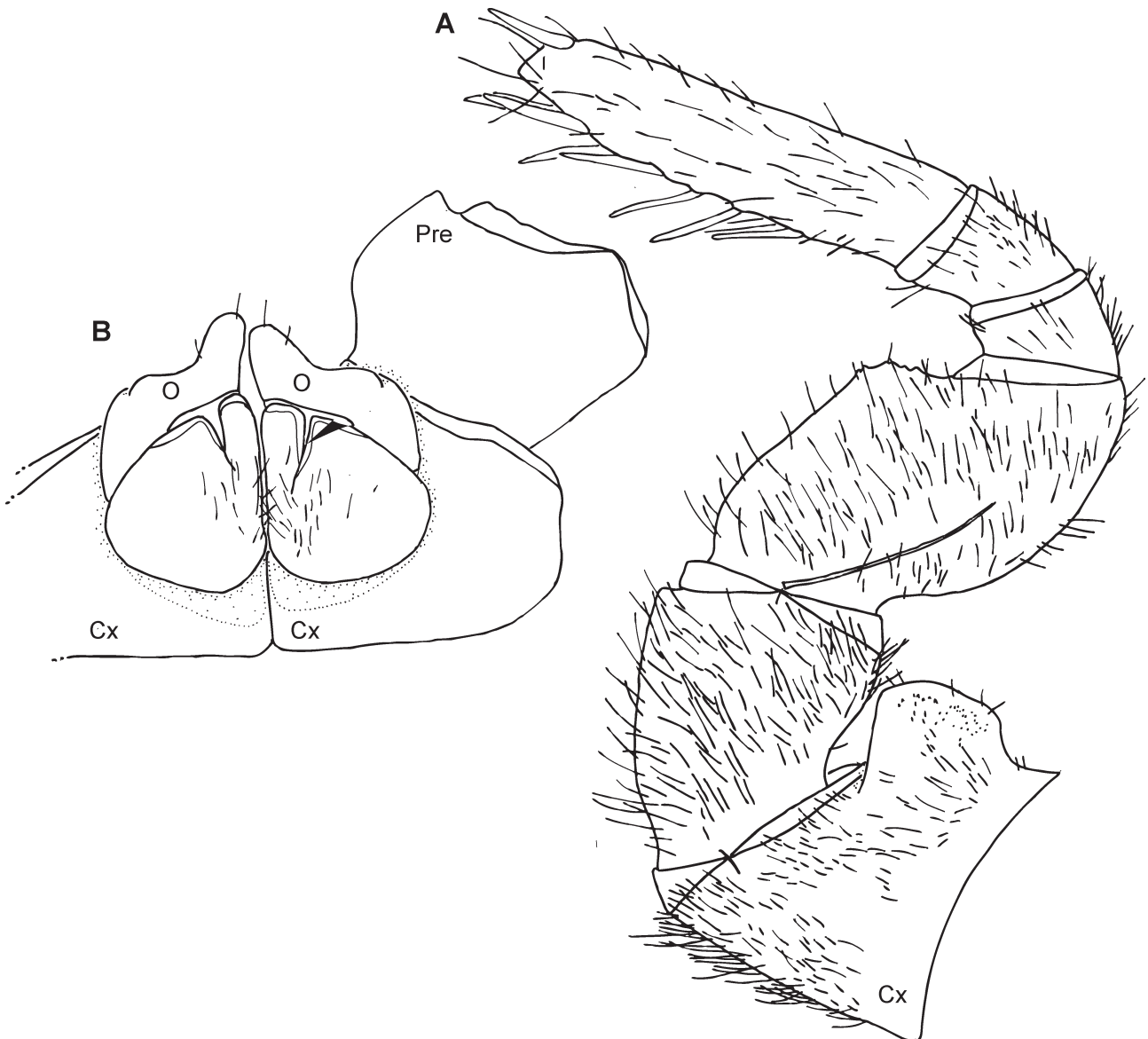
**Measurements:** Holotype male. Body length ca 32.9 mm. Width, of thoracic shield = 14.2 mm, of tergite 8 = 14.9 mm (= broadest). Height, of thoracic shield = 7.1 mm, of tergite 7 = 8.2 mm (= highest). Female: body length = ca 28.8 mm. Width, of thoracic shield = 12.6 mm, of tergite 8 = 13.6 mm (=broadest). Height, of thoracic shield = 7.6 mm, of tergite 7, 8.3 mm (= highest). **Coloration:** in preserved specimens dark green, tergites with black posterior margin. Head and collum chestnut brown. Antennae orange, legs brown (Fig. 6A).



**FIGURE 6.** Habitus multi-layer stacked photographs of *Sphaerobelum* species. A: *Sphaerobelum bolavensis* **n. sp.**; B: *Sphaerobelum phouloei* **n. sp.**; C: *Sphaerobelum denticulatum* **n. sp.**; D: *Sphaerobelum spinatum* **n. sp.**; E: *Sphaerobelum lachneeis* **n. sp.**; F: *Sphaerobelum peterjaegeri* **n. sp.**; G: *Sphaerobelum nigrum* **n. sp.**; H: *Sphaerobelum splendidum* **n. sp.**; I: *Sphaerobelum laoticum* **n. sp.** Not to scale.



**FIGURE 7.** *Sphaerobelum bolavensis* n. sp., holotype (ZMUC), left antenna, SEM, **A:** lateral view; **B:** apical disc with sensory cones. Abbreviations: **d** = apical disc; **sb** = sensilla basiconica; **sc** = sensory cones; numbers refer to antennomere number.

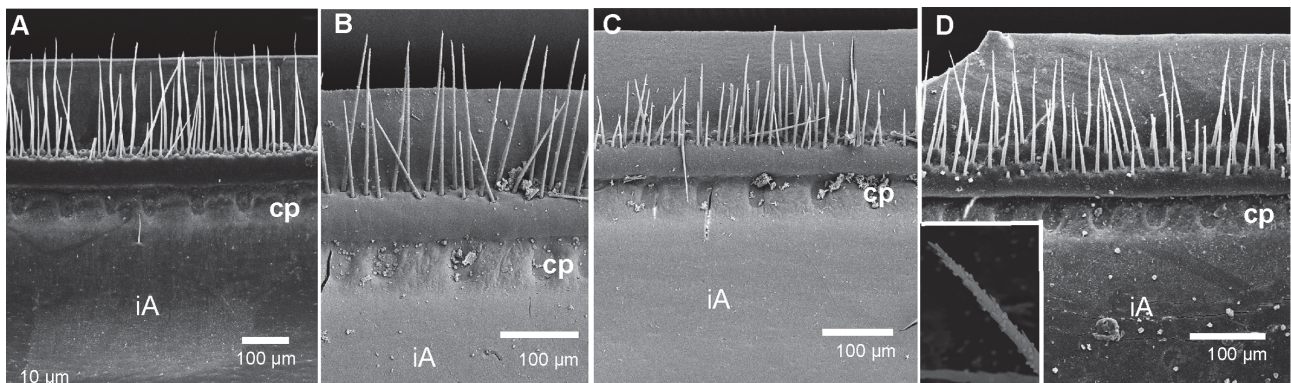


**FIGURE 8.** *Sphaerobelum bolavensis* n. sp., female paratype (ZFMK MYR8100); **A:** 9th left leg; **B:** coxa and prefemur of second leg with vulva. Abbreviations: **Cx** = coxa; **O** = operculum of vulva; **Pre** = prefemur. Not to scale.



**Head:** Eyes with >70 ocelli. Aberrant ocellus located inside antennal groove. Antennae short, with rounded joints, extending posteriorly to leg-pair 3. First antennomere with cuticular scales (Fig. 7A). Lengths of antennomeres:  $1 > 2 = 3 = 4 = 5 < 6$  (Fig. 7A). All antennomeres densely pubescent, sensilla basiconica surrounding apical disc. Shape of antennae sexually dimorphic, cylindrical in female; thickened, apically widened and slightly flattened in male (Fig. 7B). Apical disc with ca 47/52 apical cones (male) (Fig. 7B) or 30/32 (female). Apical cone shape typical of Diplopoda (Fig. 7B). Organ of Tömösváry located inside antennal groove. **Gnathochilarium:** structure typical of the order. Palpi with sensory cones arranged in clusters. **Mandibles** not dissected.

**Stigmatic plates:** first stigmatic plate widely rounded, apex well-rounded, weakly curved towards coxa 1. **Laterotergites:** laterotergite 1 strongly projecting into a sharp tip. Laterotergite 2 with a broad, stout, much shorter projection. **Collum** with glabrous surface, margins with few isolated setae. **Thoracic shield:** surface glabrous unlike tergites, setae only in grooves. Shallow grooves beset with numerous long setae, sloped towards groove with 9 continuous anterior and posterior keels. **Tergites:** surface densely setose with short setae. Tips of paratergites of midbody tergites projecting posteriorly. **Endotergum:** inner section lacking any spines or setae. Middle area with a single row of large, sparse, elliptical, cuticular impressions. Distance between impressions twice as wide as their diameter. Apically, 2 dense rows of long marginal bristles, their tips slightly protruding beyond tergal margin (Fig. 9A). Bristles not smooth, but with numerous small spicules. **Anal shield:** large, sexually dimorphic: in female weakly bell-shaped, in male strongly bell-shaped. Surface in both sexes completely covered by tiny setae. Underside with a single, short, black, locking carina, the latter located close to last laterotergite. **Legs:** leg-pair 1 with 2 ventral spines, leg-pair 2 with 4, leg-pair 3 with 5 or 6. First two leg-pairs without an apical spine. Leg-pairs 4–21 with 7–9 ventral spines and one dorso-apical spine. In leg-pair 9, femur 1.3 times, tarsus 4 times longer than wide (Fig. 8A). All podomeres densely setose. Coxa with a large and well-rounded process. Coxal process absent on leg-pair 1 and 2. Prefemur apico-mesally with a weak projection. Femur in apical part extended mesally into a dentate margin tipped with 4–6 teeth.



**FIGURE 9.** Endoterga of the body ring 9 of different *Sphaerobelum* species. **A:** *Sphaerobelum bolavensis* n. sp.; **B:** *Sphaerobelum phouloui* n. sp.; **C:** *Sphaerobelum spinatum* n. sp.; **D:** *Sphaerobelum splendidum* n. sp. Abbreviations: cp = cuticular patterns; iA = inner area.

**Female sexual characters:** vulva large, covering 2/3 of coxa, extending mesally to anterior third of prefemur (Fig. 8B). Operculum rounded, very slightly invaginated medially, mesal margin strongly projecting into a well-rounded lobe twice as long as operculum. **Subanal plate:** damaged.

**Male sexual characters:** gonopore covered with a single, undivided, circular, sclerotized plate (Fig. 10A). **Anterior telopods** (Figs 10B–D): consisting of only 3 telopoditomer above syncoxite. Telopoditomer 3 and 4 apparently fused. Telopoditomer 1 rectangular, as long as wide. Telopoditomer 2 large, half as long as telopoditomer 3. Process of telopoditomer 2 located posteriorly, visible in anterior view; process slender, projecting to half length of telopoditomer 3. Process of telopoditomer 2 conspicuously 'hooked' apically with a sharp tip. Telopoditomer 3 massive, cylindrical, straight, apically slightly tapering; posterior side with a black sclerotized spot and a small, triangular spine. Telopoditomer 1 in apical view covered with long setae. In posterior view all telopoditomer almost glabrous. **Posterior telopods** (Figs 10E, F): telopoditomer 1 short, half as long as wide. Immobile finger (process of telopoditomer 2) shorter than movable finger, consisting of telopoditomer 3 and 4. Immobile finger with a characteristic distally swollen apex; well rounded, apex therefore twice as wide as



base. Telopoditomere 3 rectangular, well rounded. Telopoditomere 4 as long as but slightly slenderer than telopoditomere 3. Telopoditomere 4 2.7 times longer than wide; apically weakly tapering, very slightly curved towards immovable finger. Telopoditomere 1 at both sides covered by setae, remaining telopoditomers in posterior view almost glabrous, in anterior view with few isolated setae except for immovable finger which is more densely setose.

**Remarks:** This species occurs in syntopy with a female of an undetermined species, Zephroniidae sp. L04b (see below).

**Derivatio nominis:** bolavensis, noun in apposition, from the Bolaven plateau in Laos where this species was discovered (Fig. 5).

### *Sphaerobelum phouloei* new species

Figures 6B, 9B, 11, 12.

*Sphaerobelum* sp. II 1 M

**Material examined:** Type specimen. 1 M holotype (ZMUC00040257) from Laos, Houaphan Province, Phou Loei, way from camp 1 to camp 2, ~ 1200 m, leg. 9.VIII.2008; S. Tarasov.

**Diagnosis:** *S. phouloei* n. sp. belongs to a group of *Sphaerobelum* species in which the mesal margin of the femur is extended in several teeth (Fig. 11B). *S. phouloei* n. sp. shares only with *S. denticulatum* n. sp. a curved telopoditomere 4 of the posterior telopods which overlaps the immovable finger (Figs 12E, F). *S. phouloei* n. sp. differs in several characters from *S. denticulatum* n. sp.: male antenna with only 30–35 apical cones (>50 in *S. denticulatum* n. sp.), prefemur mesal margin well-rounded (indentated in *S. denticulatum* n. sp.), tergites covered with short setae (glabrous in *S. denticulatum* n. sp.), legs orange (brown in *S. denticulatum* n. sp.).

**Description. Measurements:** Body length: holotype male: length ca 25.8 mm. Width, of thoracic shield 13.3 mm, of tergite 8 = 14.1 mm (= broadest). Height, of thoracic shield = 8.9 mm, of tergite 8 = 9.3 mm (= highest). **Coloration:** in preserved specimens anterior 2/3 of tergites dark olive green, posterior 1/3 black. Head, ventral side, anal shield orange (Fig. 6B). Legs and antennae orange.

**Head:** Eyes with 65–70 ocelli. Aberrant ocellus located inside antennal groove. Antennae short, with rounded joints, extending posteriorly to leg-pair 4. First antennomere with cuticular scales. Lengths of antennomeres: 1=2=3<4<5<<6. All antennomeres densely pubescent, sensilla basiconica surrounding apical disc. Last antennomere thickened, apically widened and well rounded. Apical disc with ca 36/33 apical cones. Organ of Tömösváry located inside antennal groove. **Gnathochilarium:** structure typical of the order. Palpi sensory cones located in several clusters. **Mandibles:** not dissected.

**Stigmatic plates:** first stigmatic plate widely rounded, apex well-rounded, curved towards coxa 1 (Fig. 11A). **Laterotergites:** laterotergite 1 and 2 with a broad, stout projection. **Collum:** with glabrous surface, margins with few isolated setae. **Thoracic shield:** surface glabrous unlike tergites, setae only in grooves. Shallow grooves beset with numerous long setae, slope towards groove with 3 weak anterior and 2 or 3 posterior keels. **Tergites:** anterior 2/3 of surface densely setose with short setae, posterior 1/3 glabrous. Tips of paratergites of midbody tergites projecting posteriorly (Fig. 6B). **Endotergum** (Fig. 9B): inner section lacking any spines or setae. Middle area with a single row of large, sparse, elliptical, cuticular impressions. Distance between impressions as wide as their diameter. Apically, 1–2 sparse rows of long marginal bristles, strongly protruding beyond tergal margin. Bristles not smooth, but with numerous small spinicles. **Anal shield:** large, surface completely covered by tiny setae. Underside with a single, long, black locking carina, located close to last laterotergite. **Legs:** leg-pair 1 with 2 ventral spines, leg-pair 2 with 5, leg-pair 3 with 6 or 7. First two leg-pairs without an apical spine. Leg pairs 4–21 with 9 or 10 ventral spines and one dorso-apical spine. In leg 9, femur 1.3 times, tarsus 3.7 times longer than wide (Fig. 11B). All podomeres densely setose. Coxa with a large and marginally toothed process. Coxa process absent at first leg (Fig. 11B) and sharply projecting at second (Fig. 12A). Prefemur at apical margin with a projection laterally and mesally. Lateral projection triangular and sharply edged, juxtaposed to coxal process. Femur extended mesally into a dentate margin featuring 12–14 teeth.

Female unknown.

**Male sexual characters:** gonopore covered with a single, undivided, circular, sclerotized plate (Fig. 12A). **Anterior telopods** (Figs 12B–D): consisting of 4 telopoditomers above syncoxite, but telopoditomere 3 and 4

only divided by thin suture. Telopoditomere 1 rectangular, as long as wide. Telopoditomere 2 large, almost as long as telopoditomere 3 and 4 combined. Process of telopoditomere 2 located posteriorly, not visible in anterior view. Process of telopoditomere 2 wide, projecting to half of telopoditomere 4, apically with a well-rounded tip. Telopoditomere 3 cylindrical, straight, as long as telopoditomere 4. Telopoditomere 4 cylindrical, well-rounded, posterior side with a black sclerotized spot and a small, triangular spine. Telopoditomeres 1–4 in anterior view covered with long setae. In posterior view all telopoditomeres with fewer setae. **Posterior telopods** (Figs 12E, F): telopoditomere 1 elongated, twice as long as wide. Immovable finger (process of telopoditomere 2) shorter than movable finger, consisting of telopoditomeres 3 and 4. Immovable finger with a characteristic, distally swollen apex, well rounded, apex therefore wider than base. Immovable finger in anterior view with a large spine, at tip opposite to tip of telopoditomere 4 with sclerotized spots. Telopoditomere 3 rectangular, towards immovable finger with a triangular expansion carrying a spine. Telopoditomere 4 reaching 2/3 of length of telopoditomere 3, apically strongly tapering into acute tip, very slightly curved towards immovable finger. Inner margin with single spine towards immovable finger. Telopoditomere 1 at both sides covered by setae. Telopoditomeres 2 and 3 in anterior view covered by long setae, in posterior view mostly glabrous. Telopoditomere 4 only with marginal setae.

**Derivatio nominis:** phouloei, noun in apposition, after the Phou Loei Mountain, the type locality (Fig. 5).

### *Sphaerobelum denticulatum* new species

Figures 6C, 13

**Material examined:** 1 M holotype (MHNG LT-10/12) from Laos, Oudomxai Province, ca 3 km E of Tad Lak 11, SE of Oudomxai city (= Muang Xai) (N20°36'20"; 102°01'16" E), 1020 m, undisturbed evergreen hill forest, leg. 18.IX.2010, P. Schwendinger.

**Diagnosis:** *S. denticulatum* n. sp. belongs to a group of *Sphaerobelum* species in which the mesal margin of the femur is extended with several teeth (Fig. 13A). *S. denticulatum* n. sp. shares only with *S. phouloei* n. sp. a curved telopoditomere 4 of the posterior telopods which overlaps the immovable finger (Figs 13D, E). See above for a separation of these two species.

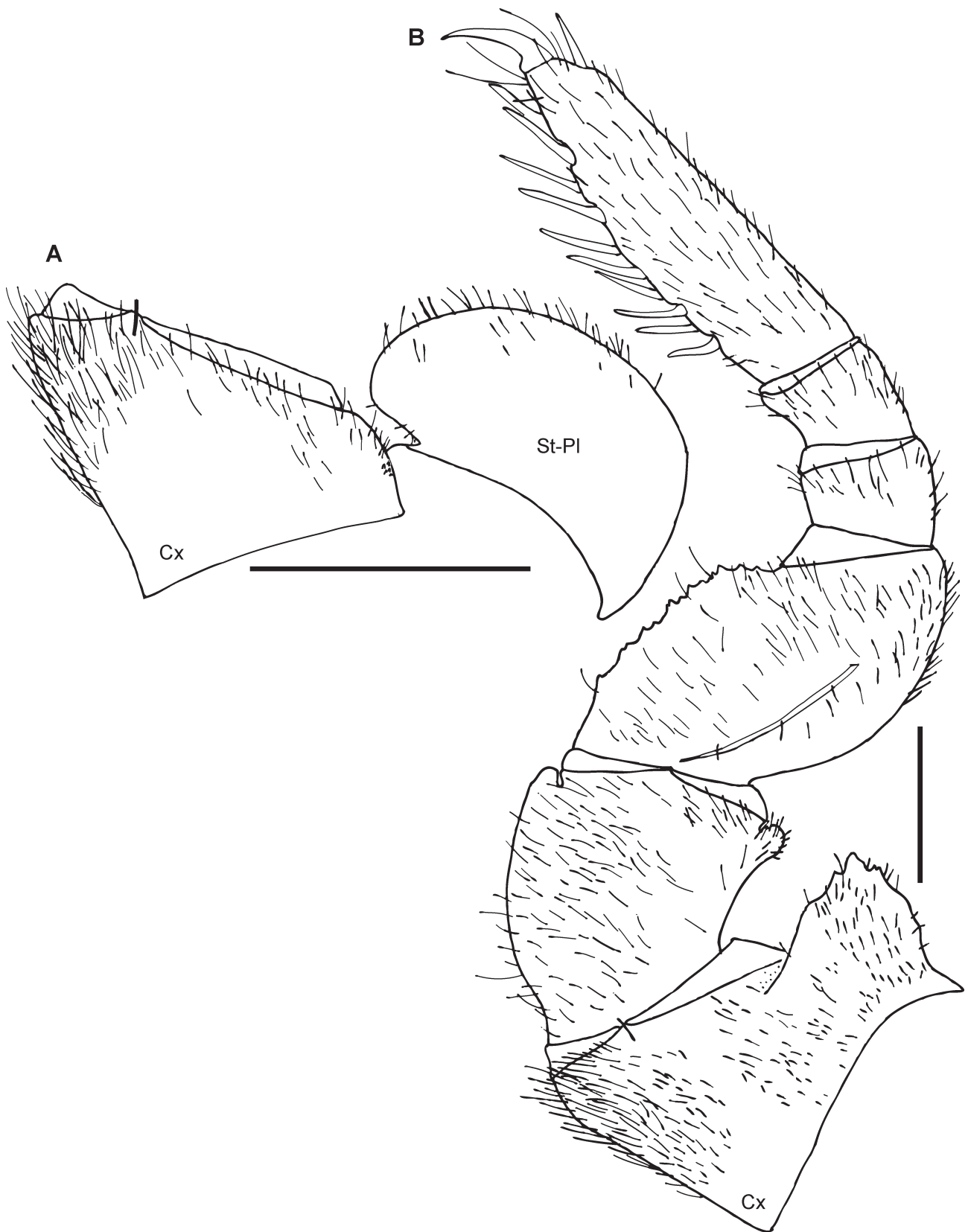
**Description. Measurements:** Body length: length ca 22.7 mm. Width, of thoracic shield = 11.5 mm (= broadest). Height, of thoracic shield = 6.3 mm, tergite 7 = 6.9 mm (= highest). **Coloration:** in preserved specimens tergites black, thoracic shield grooves and paratergite depressions dark green. Head and collum black (Fig. 6C). Antennae dirty green, antennomere 6 yellow. Legs light brown, tarsus darker.

**Head:** Eyes with ca. 55 ocelli. Antennae short, extending back to leg 3, with rounded joints. Lengths of antennomeres: 1>2=3=4=5<<6, 6 as large as 3–5 combined. All antennomeres densely pubescent, sensilla basiconica surrounding apical disc. Last antennomere thickened, cylindrical. Apical disc with 68/74 apical cones. All antennomeres covered by long setae. Organ of Tömösváry located inside antennal groove. **Gnathochilarium:** structure typical of the order. Palpi sensory cones located in single field. **Mandibles:** not dissected.

**Stigmatic plates:** first stigmatic plate rounded, apex well-rounded, straight towards coxa 1. **Laterotergites:** 1 and 2 with a short, well-rounded projection. **Collum:** with glabrous surface, margins with few isolated setae. **Thoracic shield:** surface glabrous, surface chagrinated unlike tergites, setae only in grooves. Shallow grooves beset with numerous long setae, slope towards groove with 2 or 3 weak anterior and 2 or 3 posterior keels. **Tergites:** glabrous, but entirely covered by tiny pits. Tips of paratergites of midbody tergites projecting posteriorly (Fig. 6C). **Endotergum:** inner section lacking any spines or setae. Middle area with a single row of small, circular cuticular impressions. Distance between impressions as wide as their diameter. Apically, 1–2 sparse rows of short marginal bristles, ending well before tergite margin. Bristles not smooth, but with numerous small spinicles. **Anal shield:** slightly bell shaped, surface sparsely covered by tiny setae each standing in a tiny pit. Underside with a single, black locking carina, located close to tergite margin. Locking carinae 3x size of those of tergites. **Legs:** leg-pair 1 with 3 or 4 ventral spines, leg-pair 2 with 5, leg-pair 3 with 6 or 7. First two leg-pairs without an apical spine. Leg-pairs 4–21 with 10 or 12 ventral spines and one dorso-apical spine. In leg 9 femur 1.2 times, tarsus 3.7 times longer than wide (Fig. 13A). All podomeres densely setose. Coxa with a large and marginally toothed process. Coxa process absent at first leg and sharply projecting at second. Prefemur at apical margin with a projection laterally and mesally. Lateral projection triangular and sharply edged, juxtaposed to coxal process. Femur extended mesally into a dentate margin featuring 12–14 teeth. Prefemur also with ca. 6 teeth.



**FIGURE 10.** *Sphaerobelum bolavensis* n. sp., holotype (ZMUC); **A:** coxa of second left leg with gonopore; **B:** right anterior telopod, anterior view; **C:** right anterior telopod, posterior view; **D:** right anterior telopod, lateral view; **E:** left posterior telopod, anterior view; **F:** left posterior telopod, posterior view. Abbreviations: **Syn-Cx** = syncoxite. Scale bars = 1 mm.

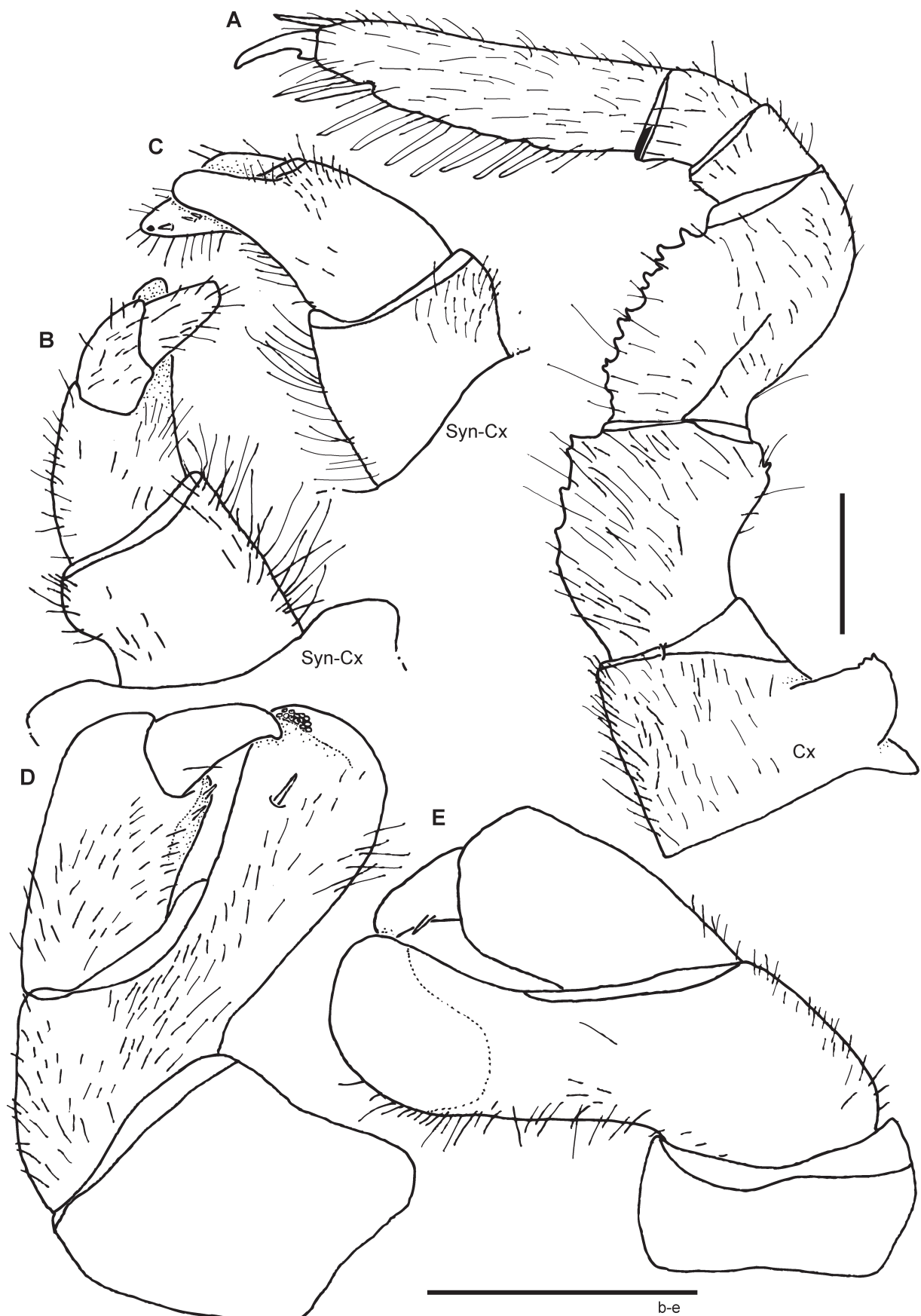


**FIGURE 11.** *Sphaerobelum phouloei* n. sp., male holotype (ZMUC); **A:** left first coxa with stigmatic plate; **B:** 9th left leg. Abbreviations: Cx = coxa; St-Pl = stigmatic plate. Scale bars = 1 mm.



**FIGURE 12.** *Sphaerobelum phouloei* n. sp., holotype (ZMUC); **A:** coxa of second left leg with gonopore; **B:** left anterior telopod, anterior view; **C:** left anterior telopod, posterior view; **D:** left anterior telopod, lateral view; **E:** right posterior telopod, anterior view; **F:** right posterior telopod, posterior view. Abbreviations: **Cx** = coxa; **Syn-Cx** = syncoxite. Scale bars = 1 mm.





**FIGURE 13.** *Sphaerobelum denticulatum* n. sp., holotype (MHNG); **A:** 9th left leg; **B:** left anterior telopod, anterior view; **C:** left anterior telopod, posterior view; **D:** left posterior telopod, anterior view; **E:** left posterior telopod, posterior view. Abbreviations: Cx = coxa; Syn-Cx = syncoxite. Scale bars = 1 mm.

Female unknown.

**Male sexual characters:** gonopore covered with a single, undivided, circular, sclerotized plate. **Anterior telopods** (Figs 13B, C): consisting of 4 telopoditomers above syncoxite. Telopoditomere 1 rectangular, as long as wide. Telopoditomere 2 large, almost as long as telopoditomere 3 and 4 combined. Process of telopoditomere 2 located posteriorly, visible mesally and apically in anterior view. Process wide, projecting to half of telopoditomere 4, apically with a well-rounded tip. Telopoditomere 3 cylindrical, straight, slightly shorter than telopoditomere 4. Telopoditomere 4 cylindrical, well-rounded, posterior side with a black sclerotized spot and three small, triangular spine. Telopoditomers 1–4 in anterior view covered with long setae. In posterior view all telopoditomers with fewer setae. **Posterior telopods** (Figs 13D, E): telopoditomere 1 slightly longer than wide. Immovable finger (process of telopoditomere 2) longer than movable finger, consisting of telopoditomers 3 and 4. Immovable finger with a characteristic, distally swollen apex, well rounded, apex therefore wider than base. Immovable finger in anterior view with a large spine, at tip opposite to tip of telopoditomere 4 with sclerotized spots. Telopoditomere 3 rectangular, towards immovable finger with a triangular expansion carrying two spines. Telopoditomere 4 reaching 2/3 of length of telopoditomere 3, much more slender, apically strongly tapering into acute tip, curved towards immovable finger. Inner margin with single spine towards immovable finger. Telopoditomere 1 at both sides covered by setae. Telopoditomers 2 and 3 in anterior view covered by long setae, in posterior view mostly glabrous. Telopoditomere 4 only with marginal setae.

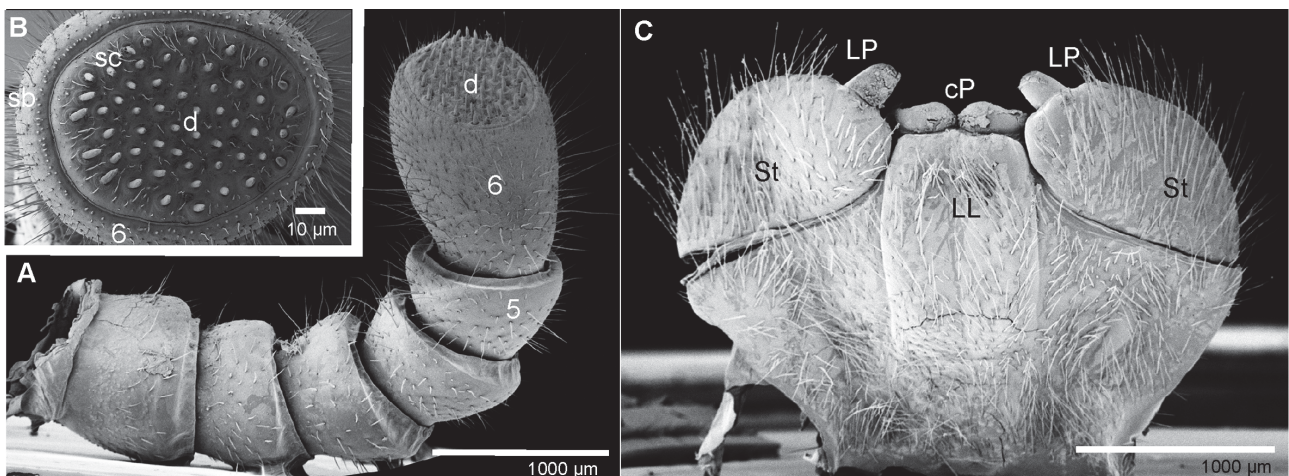
**Derivatio nominis:** denticulatum, noun in apposition, after the dentate mesal margin of the femur and prefemur.

### *Sphaerobelum spinatum* new species

Figures 6D, 9C, 14, 15, 16

**Material examined:** Type specimens. 1 M holotype (ZMUC00040258) from Laos, Vientiane Province, Phou Khao Khouay (N18°20.369'N, 102°48.523'E), 700–800 m, strongly disturbed primary evergreen forest, leg. 26–31.V.2008, A. Solodovnikov & J. Pedersen; 1 F paratype; ZMUC00040259; same data as paratype; 1 M, 1 F paratype (ZFMK MYR8101 & MYR8102), same data as holotype.

**Diagnosis:** *S. spinatum* n. sp. belongs to a group of *Sphaerobelum* species in which the mesal margin of the femur is extended with several teeth (Fig. 15B). *S. spinatum* n. sp. shares only with *S. cattense* and *S. konkakinhense* a straight telopoditomere 4 (Figs 16E, F). *S. spinatum* n. sp. differs in several characters from both other species: mesal margin of prefemur with indentations like the femur (Fig. 15B), male antenna with <60 apical cones (>70 in *S. denticulatum* n. sp.), tergites shiny, but setose (tergites covered with setose pits in the other species), first laterotergite strongly projecting, extended into a sharp tip (first laterotergite only weakly projecting in the other two species).



**FIGURE 14.** *Sphaerobelum spinatum* n. sp., holotype (ZMUC), SEM, **A:** left antenna, lateral view; **B:** apical disc with sensory cones; **C:** gnathochilarium, ventral view. Abbreviations: **cP** = central pads; **d** = apical disc; **LL** = lamellae linguales; **LP** = lateral palpus; **sb** = sensilla basiconica; **sc** = sensory cones; **St** = stipes; numbers refer to antennomere number.

**Description.** Based on holotype and both paratypes.

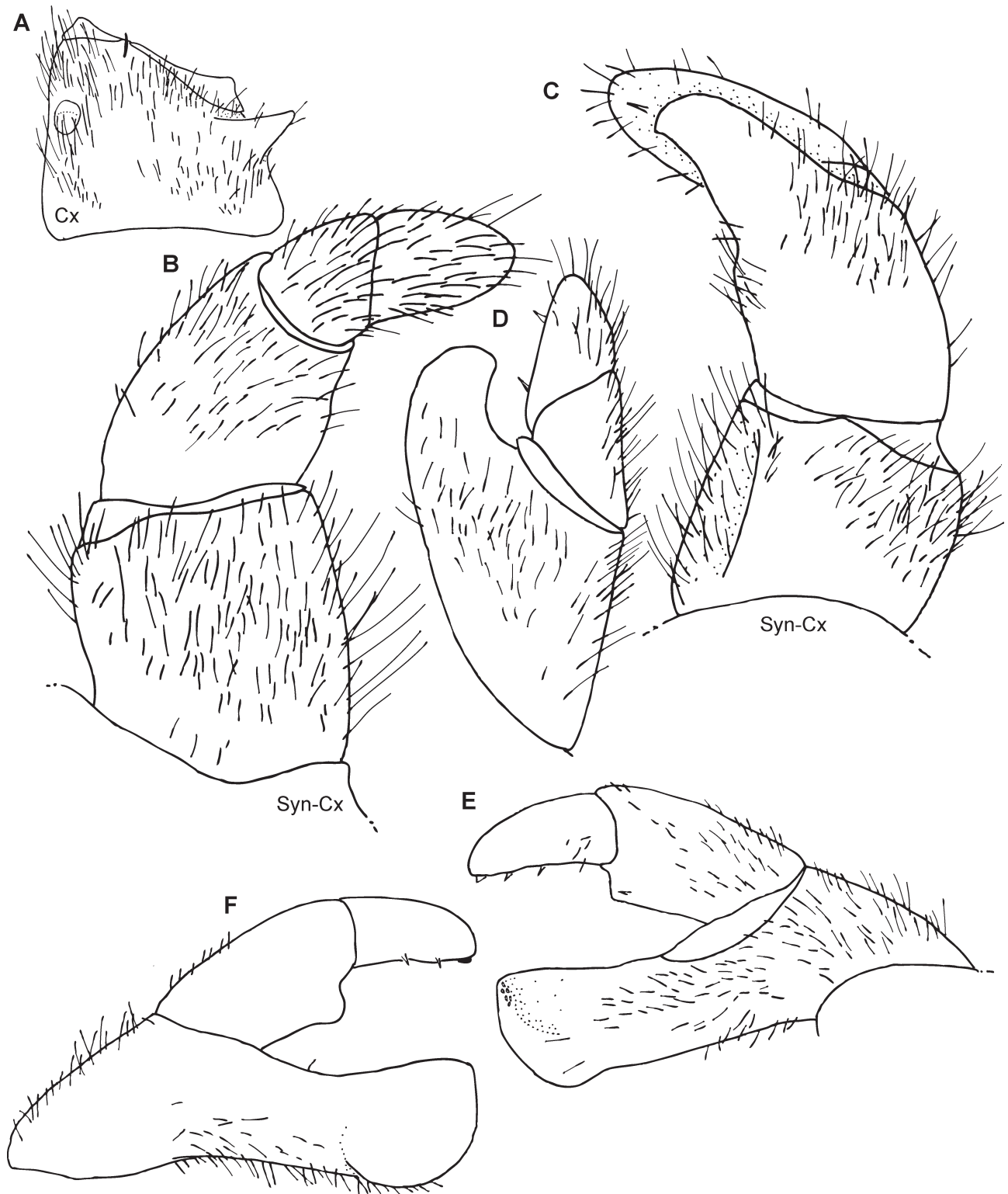
**Measurements:** Body length: holotype male: length ca 26.9 mm. Width, of thoracic shield = 13.6 mm (= broadest). Height, of thoracic shield = 7.5 mm (= highest). Female: length ca 32.5 mm. Width, of thoracic shield = 14.5 mm, of tergite 7 = 15.7 mm (=broadest). Height, of thoracic shield = 7.7 mm, of tergite 9 = 9.1mm (= highest). **Coloration:** in preserved specimens black, paratergite depressions and groove of thoracic shield dark green (Fig. 6D). Antennae brown-orange, legs light brown, but prefemur and femur green.



**FIGURE 15.** *Sphaerobelum spinatum* n. sp., **A, B:** holotype (ZMUC); **C, D:** female paratype (ZFMK MYR8102); **A:** coxa of first left leg with first stigmatic plate; **B:** 9th left leg; **C:** coxa and prefemur of second leg with vulva; **D:** subanal plate. Abbreviations: Cx = coxa; O = operculum of vulva; Pre = prefemur; St-PI = stigmatic plate. Not to scale.

**Head:** Eyes with >60 ocelli. Aberrant ocellus located inside antennal groove. Antennae short, with rounded joints, extending posteriorly to leg-pair 5. Lengths of antennomeres: 1>2=3=4=5<<6 (Fig. 14A). All antennomeres

densely pubescent, sensilla basiconica surrounding apical disc. Shape of antennae sexually dimorphic, cylindrical in female, thickened, apically widened and slightly flattened in male (Fig. 14B). Apical disc with ca 52/52 apical cones (male) (Fig. 14b), or 30–36 (female). Organ of Tömösváry located inside antennal groove. **Gnathochilarium:** Damaged. Structure typical of the order (Fig. 14C). Palpi with sensory cones arranged in single field. Rudimentary lateral palps not visible.



**FIGURE 16.** *Sphaerobelum spinatum* n. sp., holotype (ZMUC); **A:** coxa of second left leg with gonopore; **B:** left anterior telopod, anterior view; **C:** left anterior telopod, posterior view; **D:** left anterior telopod, lateral view; **E:** right posterior telopod, anterior view; **F:** right posterior telopod, posterior view. Abbreviations: Cx = coxa; Syn-Cx = syncoxite. Not to scale.



**Mandibles:** not dissected.

**Stigmatic plates:** first stigmatic plate rounded, apex well-rounded, straight towards coxa 1 (Fig. 15A). **Laterotergites:** laterotergite 1 strongly projecting into a sharp tip. Laterotergite 2 with a broad, stout, much shorter projection. **Collum:** with glabrous surface, margins with few isolated setae. **Thoracic shield:** surface glabrous but covered with tiny pits, setae only in grooves. Slope towards groove without anterior keels but with 4 or 5 posterior keels. **Tergites:** surface anterior half densely setose with short setae, posterior half glabrous, shiny. Tips of paratergites of midbody tergites projecting posteriorly (Fig. 6D). **Endotergum:** inner section lacking any spines or setae. Middle area with a single row of large, sparse, elliptical, cuticular impressions. Distance between impressions twice as wide as their diameter. Apically, 2-3 dense rows of long marginal bristles, the tips of the longest setae slightly protruding beyond tergal margin (Fig. 9C). Bristles not smooth, but with numerous small spinicles. **Anal shield:** large, in both sexes well-rounded. Surface in both sexes completely covered by tiny setae located in small pits. Underside with a single, short, black, locking carina, located close to last laterotergite. **Legs:** leg-pair 1 with 2 or 3 ventral spines, leg-pair 2 with 6, leg-pair 3 with 7 or 8. First two leg-pairs without an apical spine. Leg-pairs 4–21 with 10 ventral spines and one dorso-apical spine. In leg 9, femur 1.6 times, tarsus 3.7 times longer than wide (Fig. 15B). All podomeres densely setose. Coxa with a large and marginally toothed process. Coxa process absent at first leg (Fig. 15A) and sharply projecting at second (Figs 15C, 16A). Prefemur at apical margin with a projection laterally and mesally. Lateral projection triangular and sharply edged, juxtaposed to coxal process. Femur extended mesally into a dentate margin featuring 12–14 teeth.

**Female sexual characters:** female gravid. Vulva large, covering 2/3 of coxa, extending mesally to anterior third of prefemur (Fig. 15C). Operculum rounded, very slightly invaginated medially, mesal margin strongly projecting into a well-rounded lobe twice as high as remaining operculum. **Subanal plate:** large and wide, divided by a suture into two halves. Densely setose (Fig. 15D).

**Male sexual characters:** gonopore covered with a single, undivided, circular, sclerotized plate (Fig. 16A). **Anterior telopods** (Figs 16B–D): consisting of 4 telopoditomers above syncoxite. Telopoditomere 1 rectangular, as long as wide. Telopoditomere 2 large, as long as telopoditomere 1. Process of telopoditomere 2 located posteriorly, not visible in anterior view. Process of telopoditomere 2 wide, well-rounded, projecting to half of telopoditomere 3. Telopoditomere 3 small, slightly shorter than telopoditomere 4. telopoditomere 4 cylindrical, well-rounded, posterior side with two small spines. All telopoditomers covered with long setae. **Posterior telopods** (Figs 16E, F): telopoditomere 1 short, half as long as wide. Immovable finger (process of telopoditomere 2) as long as movable finger, consisting of telopoditomers 3 and 4. Immovable finger with a characteristic, distally swollen apex, well rounded apically, apex only slightly wider than base. Telopoditomere 3 rectangular, well rounded, apically with a well-rounded extension carrying a small spine. Telopoditomere 4 only slightly shorter and slightly more slender than telopoditomere 3, 2.1 times longer than wide, apically weakly tapering, straight, not curved, with 3 small spines at margin towards immovable finger. In anterior view telopoditomere 1–3 covered by setae, in posterior view telopoditomers 2–4 mostly glabrous except for a few setae at the margins.

**Derivatio nominis:** spinatum, noun in apposition, after the sharp process of the first laterotergite.

### ***Sphaerobelum lachneeis* new species**

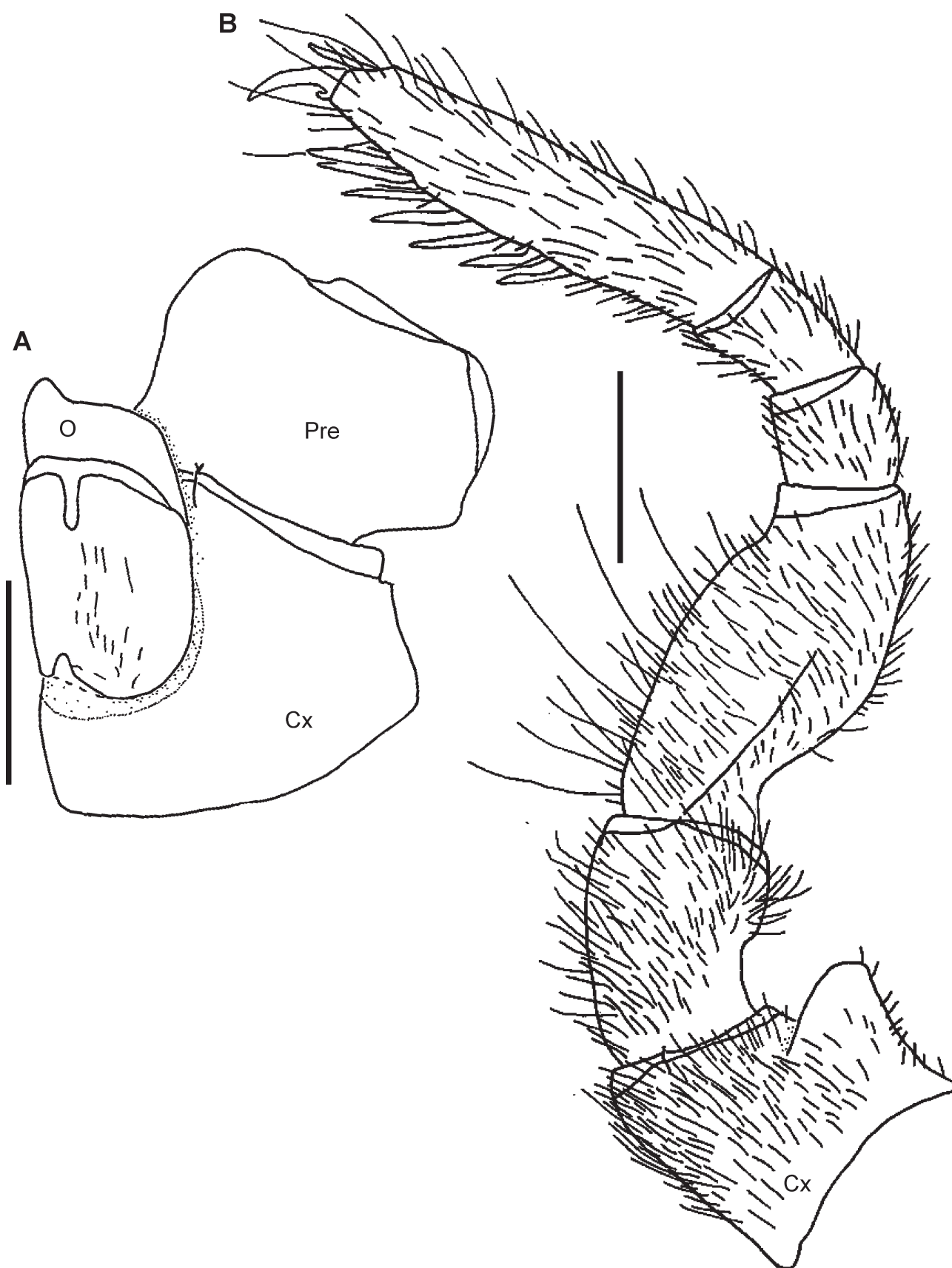
Figures 6E, 17, 18

**Material examined:** Type specimens. 1 M holotype (MHNG LT-10/12) from Laos, Oudomxai Province, ca 3 km E of Tad Lak 11, SE of Oudomxai city (= Muang Xai), (N20°36'20", 102°01'16" E), 1020 m, primary forest, leg. 18.IX.2010, P. Schwendinger. 1 F paratype (MHNG LT-10/12), same data as holotype; 1 M paratype (ZFMK MYR8099), same data as holotype.

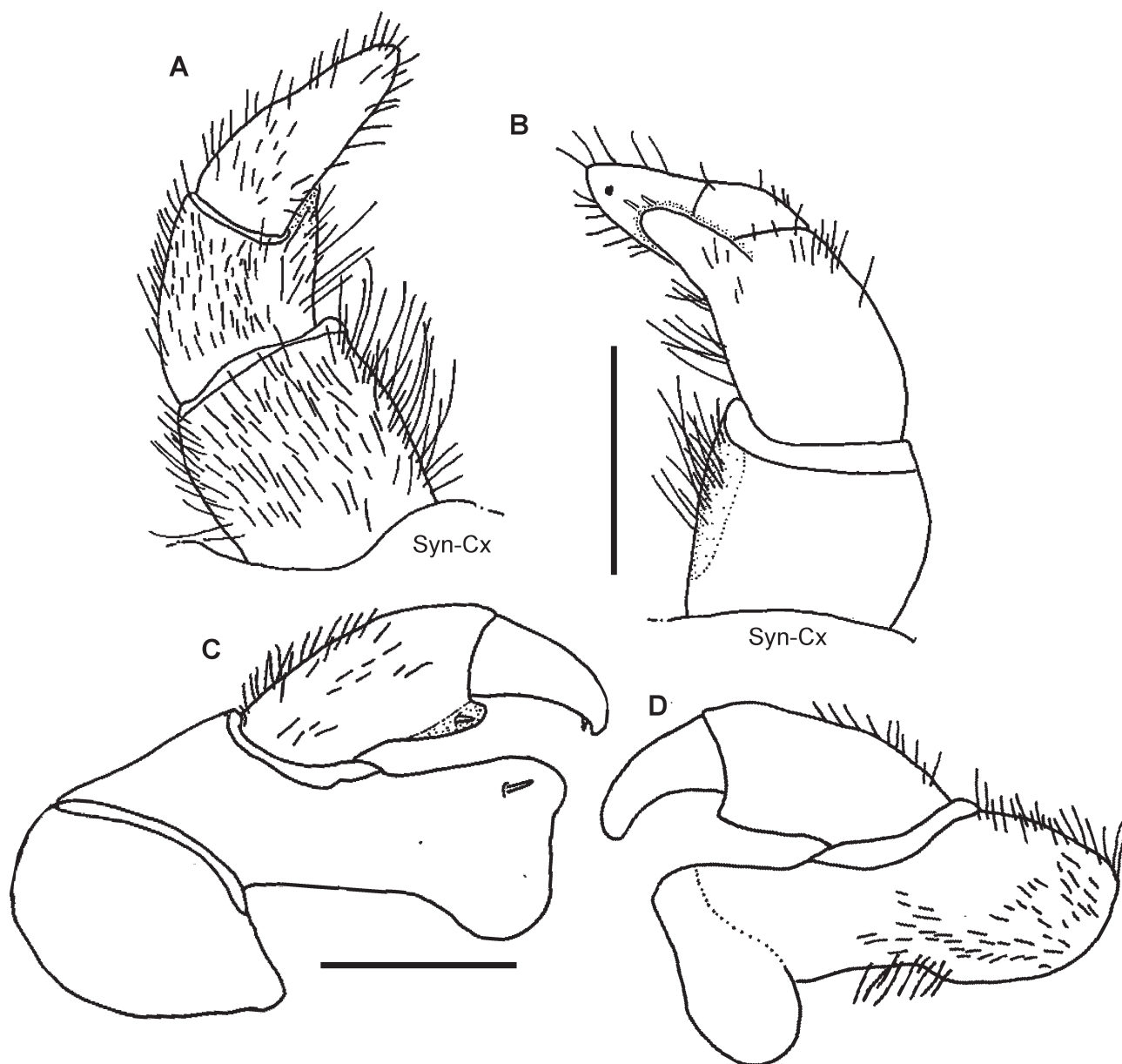
**Diagnosis:** *S. lachneeis* **n. sp.** belongs to a group of *Sphaerobelum* species in which the mesal margin of the femur is unmodified (Fig. 17B). *S. lachneeis* **n. sp.** shares only with *S. separatum*, *S. truncatum* and *S. peterjaegeri* **n. sp.** the absence of a "hook" at telopoditomere 4 (of the posterior telopods Figs 18C, D). *S. lachneeis* **n. sp.** differs from all those species in the presence of an only weakly separated telopoditomere 3 and 4 of the anterior telopods (Figs 18A, B), very long setae at the tergites (Fig. 6E), and a very long mesal extension at the apex of the immovable finger of the posterior telopods (Fig. 18C).

**Description.** Based on holotype and both paratypes.





**FIGURE 17.** *Sphaerobelum lachneeis* n. sp., female paratype (MHNG); **A:** coxa and prefemur of second leg with vulva; **B:** 9th left leg. Abbreviations: **Cx** = coxa; **O** = operculum of vulva; **Pre** = prefemur. Scale bars = 1 mm.



**FIGURE 18.** *Sphaerobelum lachneeis* n. sp., holotype (MHNG); **A:** left anterior telopod, anterior view; **B:** left anterior telopod, posterior view; **C:** left posterior telopod, anterior view; **D:** left posterior telopod, posterior view. Abbreviations: **Syn-Cx** = syncoxite. Scale bars = 1 mm.

**Measurements:** Body length: holotype male: length ca 23.5 mm. Width, of thoracic shield = 11.8 mm, of tergite 8 = 12.4 mm (= broadest). Height, of thoracic shield = 6.8 mm (= highest). Female: length ca 26.9 mm. Width, of thoracic shield = 13.3 mm, of tergite 7 = 13.9 mm (=broadest). Height, of thoracic shield = 7.5 mm, of tergite 8 = 8.5mm (= highest). **Coloration:** in preserved specimens dark olive-green, paratergite depressions and groove of thoracic shield lighter green, as ventral side (Fig. 6E). Antennae green, legs brown- olive greenish.

**Head:** densely setose with very long setae (setae as long as width of tergite). Eyes with ca. 50 ocelli. Aberrant ocellus located inside antennal groove. Antennae short, with rounded joints, extending posteriorly to leg-pair 3. Lengths of antennomeres:  $1 > 2 = 3 = 4 = 5 < 6$ . All antennomeres densely pubescent, sensilla basiconica surrounding apical disc. Antennomere 6 cylindrical in both sexes. Apical disc with ca 40/42 apical cones (male), or 31/29 (female). Organ of Tömösváry located inside antennal groove. **Gnathochilarium:** structure typical of the order. Palpi with sensory cones arranged in clusters. **Mandibles:** not dissected.

**Stigmatic plates:** first stigmatic plate rounded, apex well-rounded, straight towards coxa 1. **Laterotergites:** laterotergite 1 weakly projecting into a rounded. Laterotergite 2 with a broad, stout, much shorter projection.

**Collum:** surface like those of tergites, densely setose with very long setae. **Thoracic shield:** surface like those of tergites. Slope towards groove continuous row of 9 keels. **Tergites:** surface densely setose with very long setae, each starting from a small pit. Tips of paratergites of midbody tergites projecting posteriorly (Fig. 6E). **Endotergum:** inner section lacking any spines or setae. Middle area with a single, dense row of large, shallow, elliptical, cuticular impressions. Distance between impressions shorter than their diameter. Apically, 1-2 dense rows of long marginal bristles, the tips of the longest setae slightly protruding beyond tergal margin. Bristles not smooth, but with numerous small spinicles. **Anal shield:** large, in both sexes well-rounded. Surface in both sexes completely covered by setae located in small pits. Longer setae like the ones found on the tergites in the anterior part, short setae in the posterior part. Underside with a single, black, locking carina reaching 3x the length of those of the tergites, located close to the margin. **Legs:** leg-pair 1 with 2 ventral spines, leg-pair 2 with 3, leg-pair 3 with 5 or 6. First two leg-pairs without an apical spine. Leg-pairs 4–21 with only 6 or 7 ventral spines and one dorso-apical spine. In leg 9, femur 1.7 times, tarsus 4.7 times longer than wide (Fig. 17B). All podomeres densely setose. Coxa with a large and well-rounded process. Coxa process absent at first leg, sharply projecting at second (Fig. 17A). Prefemur and femur without any teeth.

**Female sexual characters:** Vulva small, covering mesal 1/3 of coxa, extending mesally to anterior fifth of prefemur (Fig. 17A). Operculum rounded, mesal margin projecting into a well-rounded lobe 1/3 as high as remaining operculum. **Subanal plate:** large and wide, undivided. Densely setose.

**Male sexual characters:** gonopore covered with a single, undivided, circular, sclerotized plate. **Anterior telopods** (Figs 18A, B): consisting of three telopoditomere above syncoxite. Last telopoditomere divided by a suture still visible in lateral and posterior view. Telopoditomere 1 rectangular, as long as wide. Telopoditomere 2 large, but shorter than telopoditomere 1 or 3. Process of telopoditomere 2 located posteriorly, not visible in anterior view. Process of telopoditomere 2 wide, well-rounded, projecting to half of telopoditomere 3. Telopoditomere 3 massive, conical, well-rounded, posterior side with two small spines and a black sclerotized spot. All telopoditomeres covered with long setae. **Posterior telopods** (Figs 18C, D): telopoditomere 1 short, half as long as wide. Immobile finger (process of telopoditomere 2) shorter than movable finger, consisting of telopoditomeres 3 and 4. Immobile finger with a characteristic, distally swollen apex, bone-shaped, well rounded apically, with a strong basal swelling, apex twice as wide as base. Telopoditomere 3 rectangular, well rounded, apically with a well-rounded extension carrying a small spine. Telopoditomere 4 only slightly shorter and slightly more slender than telopoditomere 3, 2.4 times longer than wide, apically weakly tapering, minimally curved, with one small spines at margin towards immobile finger. In anterior view telopoditomere 1–3 covered by setae (not drawn at telopoditomere 1 and 2), in posterior view telopoditomeres 2–4 mostly glabrous except for a few setae at the margins.

**Derivatio nominis:** lachneeis, noun in apposition, after lachnos (= wool).

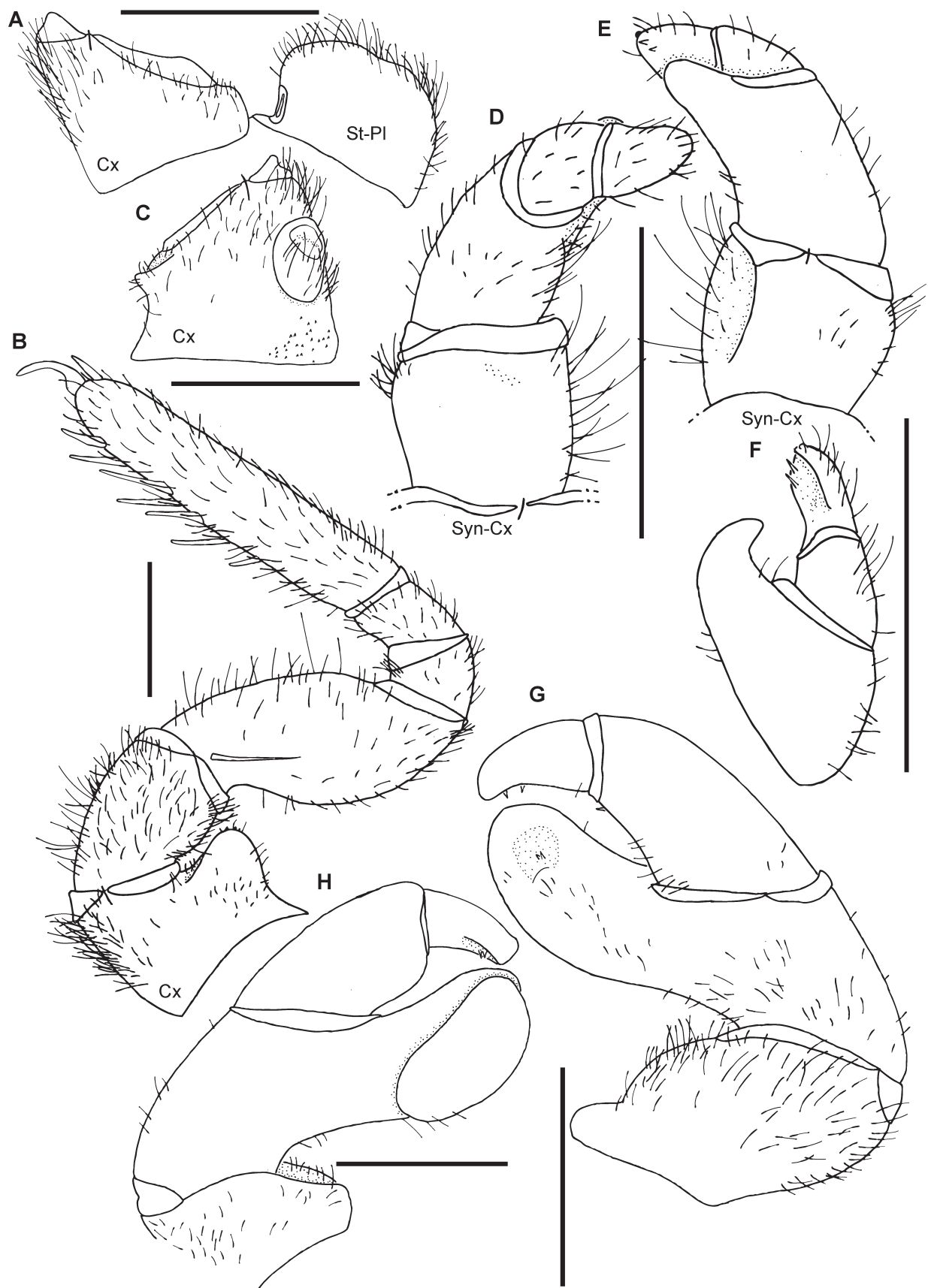
### *Sphaerobelum peterjaegeri* new species

Figures 6F, 19

**Material examined:** 1 M, holotype (SMF SD553) from Laos, Luang Prabang Province, SE Luang Prabang, Nam Khan, Ban Pak Bak, Houay Kho, 328 m, (N19°44'09.1", 102°16'37.5"E), bank of stream, under stone, moist sand and gravel, leg. 28.II.2008, P. Jäger.

**Diagnosis:** *S. peterjaegeri* n. sp. belongs to a group of *Sphaerobelum* species in which the mesal margin of the femur is unmodified (Fig. 19B). *S. peterjaegeri* n. sp. shares only with *S. separatum*, *S. truncatum* and *S. lachneeis* n. sp. the absence of a "hook" at telopoditomere 4 of the posterior telopods (Figs 19G, H). *S. peterjaegeri* n. sp. differs from *S. separatum* in the absence of a lateral extension on podomere 3 of the anterior telopod, as well as the absence of an incurved process on telopoditomere 4 of the posterior telopods. *S. peterjaegeri* n. sp. is very similar to *S. truncatum*, but differs in several characters: <70 apical cones on the antenna (>80 in *S. truncatum*), antennae and legs orange-red (yellow in *S. truncatum*), femur 1.7 times longer than wide (2.0 times longer than wide in *S. truncatum*).

**Description. Measurements:** Body length: holotype male: length ca 23.8 mm. Width of thoracic shield = 11.6 mm (= broadest). Height of thoracic shield = 6.9 mm (= highest). **Coloration:** in preserved specimens brown to orange (Fig. 6F). Collum dark olive brown, same as head. Antennae and legs orange.



**FIGURE 19.** *Sphaerobelum peterjaegeri* n. sp., holotype (SMF); **A:** coxa of first left leg with first stigmatic plate; **B:** 9th left leg; **C:** coxa of second left leg with gonopore; **D:** left anterior telopod, anterior view; **E:** left anterior telopod, posterior view; **F:** left anterior telopod, lateral view; **G:** right posterior telopod, anterior view; **H:** right posterior telopod, posterior view. Abbreviations: Cx = coxa; St-Pl = stigmatic plate; Syn-Cx = syncoxite. Scale bars = 1 mm.

**Head:** Eyes with ca. 60 ocelli. Aberrant ocellus located inside antennal groove. Antennae short, with rounded joints, extending posteriorly to leg-pair 3. First antennomere with cuticular scales. Lengths of antennomeres: 1=2=3=4=5<<6. Shape of apical joint thickened, apically widened. Apical disc with ca 66/68 apical cones. Organ of Tömösváry located inside antennal groove. **Gnathochilarium:** structure typical of the order. Palpi with sensory cones arranged in a single field. **Mandibles:** not dissected.

**Stigmatic plates:** first stigmatic plate well-rounded (Fig. 19A). **Laterotergites:** laterotergite 1 slightly projecting into a sharp but short tip. Laterotergite 2 with a broad, stout, much shorter projection. **Collum:** with few isolated setae on entire surface. **Thoracic shield:** surface hirsute like tergites, longer setae only in grooves. Shallow grooves beset with numerous long setae, slope towards groove with 4 or 5 posterior keels, anterior keels absent. **Tergites:** surface densely setose with short setae. Tips of paratergites of midbody tergites projecting posteriorly (Fig. 6F). **Endotergum:** posterior margin conspicuously tessellated. Inner section without any setae or spines. Middle area with a single row of dense elliptical, cuticular impressions, distance between impressions slightly smaller than their diameter. Apically, 2-3 dense rows of short marginal bristles, the longest just protruding up to 2/3 of the distance to tergal margin. Bristles not smooth, but with numerous small spicules. **Anal shield:** well-rounded. Surface completely covered by tiny setae. Underside with a single, very long black, locking carina, located close to last laterotergite. **Legs:** leg-pair 1 with 2 ventral spines, leg-pair 2 with 4, leg-pair 3 with 6. First two leg-pairs without an apical spine. Leg-pairs 4–21 with 7–10 ventral spines and one dorso-apical spine. In leg 9, femur 1.7 times, tarsus 4.6 times longer than wide (Fig. 19B). All podomeres densely setose. Coxa with a large and well-rounded process. Coxal process absent at leg 1 and 2 (Figs 19A, C).

Female unknown

**Male sexual characters:** gonopore covered with a single, undivided, circular, sclerotized plate (Fig. 19C). **Anterior telopods** (Figs 19D–F): consisting of 4 telopoditomers above syncoxite. Telopoditomere 1 rectangular, as long as wide. Telopoditomere 2 large, as long as telopoditomere 1. Process of telopoditomere 2 located posteriorly, visible in anterior view. Process of telopoditomere 2 wide, projecting to half of telopoditomere 4, apically with a well-rounded tip. Telopoditomere 3 cylindrical, straight, apically slightly tapering, as long as telopoditomere 4. Telopoditomere 4 cylindrical, apex slightly bent posteriorly. Posterior side with a black sclerotized spot and two small, triangular spines. Telopoditomers 1–4 with only few, mainly marginal long setae. **Posterior telopods** (Figs 19G, H): telopoditomere 1 elongated, twice as long as wide. Immovable finger (process of telopoditomere 2) shorter than movable finger, consisting of telopoditomers 3 and 4. Immovable finger with a characteristic, distally swollen apex, well rounded, apex not expanded, only slightly wider than base. Telopoditomere 3 elongated, towards immovable finger close to apex with a slight extension carrying a small spine. Telopoditomere 4 shorter and more slender than telopoditomere 3, 2.1 times longer than wide, apically weakly tapering, very slightly curved towards immovable finger, at inner margin with two small spines. Telopoditomere 1 and 2 at both sides covered by setae. Telopoditomere 3 at base at inner margin with a few setae, remaining parts of telopoditomers 3 and 4 almost glabrous.

**Derivatio nominis:** peterjaegeri, noun in apposition, after the Arachnologist Peter Jäger, great collector of arthropods in Laos and other countries.

### *Sphaerobelum nigrum* new species

Figures 6G, 20, 21

**Material examined:** Type specimens: 1 M holotype (SMF) from Laos, Champasak Province, Muang Bachieng, Ban Lak 35, Tad Etu (N15°11'37.7", 106°06'06.3"E), 810 m, coffee plantation with remnant of secondary forest, leg. in vegetation, at night, by hand; 16.XI.2012; P. Jäger.

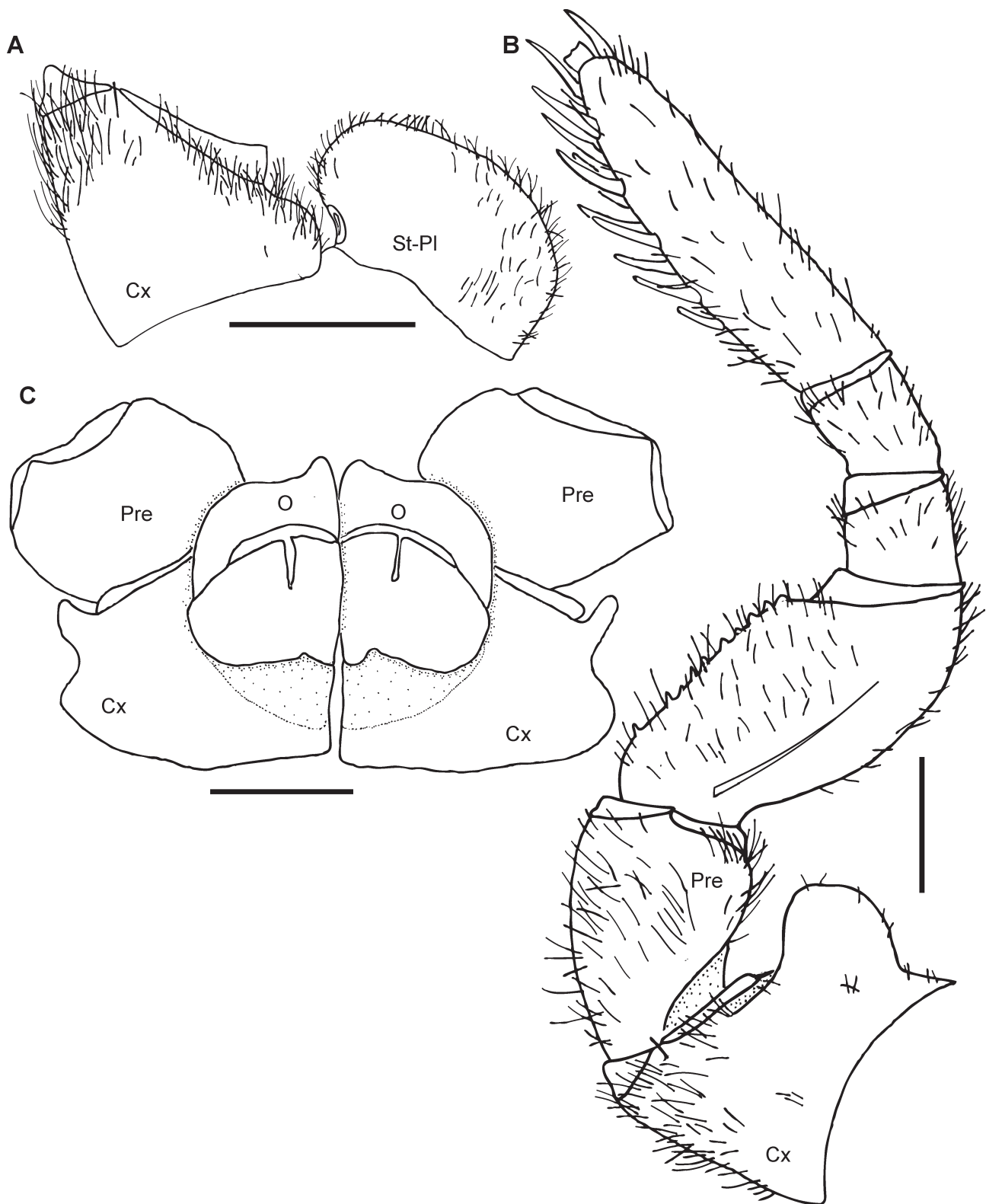
**Paratype:** 1 F (SMF) from Laos, Champasak Province, Muang Bachieng, Ban Lak 35, Tad Etu (N15°11'37.7", 106°06'06.3"E), 810 m, coffee plantation with remnant of secondary forest, close to river, at rock, leg. at day, by hand, 25.XI.2009, P. Jäger & S. Bayer.

**Diagnosis:** *S. nigrum* n. sp. belongs to a group of *Sphaerobelum* species in which the mesal margin of the femur is modified (Fig. 20B). *S. nigrum* n. sp. shares only with *S. hirsutum*, *S. clavigerum*, *S. splendidum* n. sp. and *S. schwendingeri* n. sp. the presence of a "hook" at telopoditomere 4 of the posterior telopods (Figs 21E, F). *S. nigrum* n. sp. differs from *S. hirsutum* in the presence of glabrous tergites, from *S. clavigerum* in the presence of a

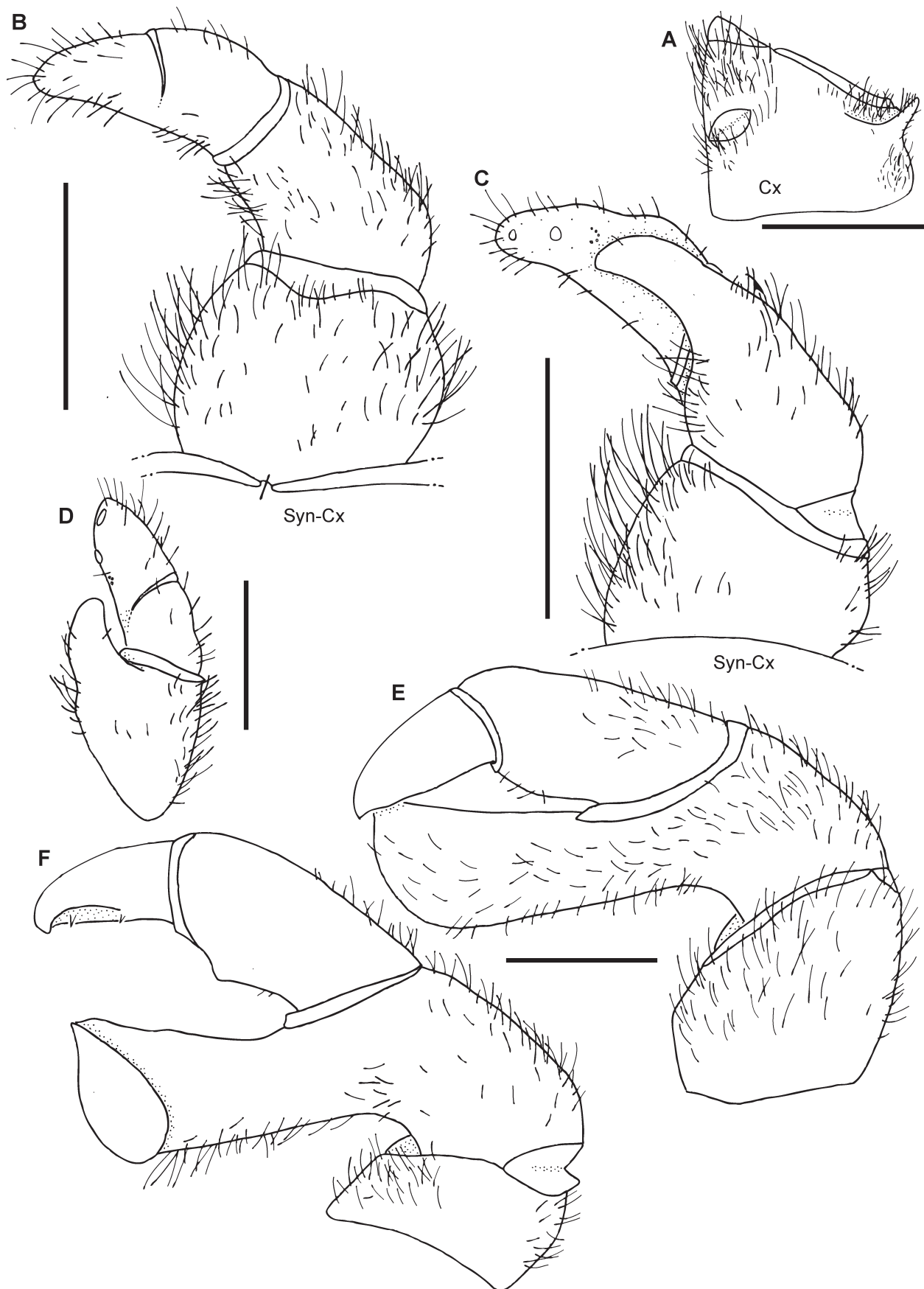


short locking carina on the anal shield. Differs from *S. splendidum* **n. sp.** and *S. schwendingeri* sp. in the presence of an axe-shaped antennomere 6, and the presence of only a short hook at the telopoditomere 4 (Figs 21E, F) of the posterior telopods (strongly curved telopoditomere 4 in the other two species).

**Description.** Based on holotype male and paratype female.



**FIGURE 20.** *Sphaerobelum nigrum* **n. sp.**, holotype (SMF); **A:** coxa of first left leg with first stigmatic plate; **B:** 9th left leg; **C:** coxa and prefemur of second leg with vulva. Abbreviations: **Cx** = coxa; **O** = operculum of vulva; **Pre** = prefemur; **St-Pl** = stigmatic plate. Scale bars = 1 mm.



**FIGURE 21.** *Sphaerobelum nigrum* n. sp., holotype (SMF); **A**: coxa of second left leg with gonopore; **B**: right anterior telopod, anterior view; **C**: right anterior telopod, posterior view; **D**: right anterior telopod, lateral view; **E**: right posterior telopod, anterior view; **F**: left posterior telopod, posterior view. Abbreviations: **Syn-Cx** = syncoxite. Scale bars = 1 mm.

**Measurements:** Body length: holotype male: length ca 27.8 mm. Width, of thoracic shield = 16.1 mm, of tergite 7 = 16.8 mm (= broadest). Height, of thoracic shield = 9.8 mm, of tergite 7 = 10.1 mm (= highest). Female: length ca 34.7 mm. Width, of thoracic shield = 15.7 mm, of tergite 7 = 17.4 mm (= broadest). Height of thoracic shield = 9.3 mm, of tergite 7 = 9.8 mm (= highest). **Coloration:** in preserved specimens yellow with dark brown spots or black spots/bands. Head and collum black (Fig. 6G). Antennae and legs dark brown to black.

**Head:** Eyes with ca. 55 ocelli. Antennae short, with rounded joints, extending posteriorly to leg-pair 4. Lengths of antennomeres: 1=2=3=4=5<<6. All antennomeres densely pubescent, sensilla basiconica surrounding apical disc. Last antennomere thickened, apically widened, axe-shaped. Apical disc with 91/89 apical cones (male), 74/78 (female). Organ of Tömösváry located inside antennal groove. **Gnathochilarium:** structure typical of the order. Palpi sensory cones located in single field. **Mandibles:** not dissected.

**Stigmatic plates:** first stigmatic plate widely rounded, apex well-rounded, curved towards coxa 1 (Fig. 20A). **Laterotergites:** laterotergite 1 and 2 elongated into a long, sharply pointed process. **Collum:** with glabrous surface, margins with few isolated setae. **Thoracic shield:** surface glabrous, but covered with small pits like tergites, setae only in grooves. Shallow grooves beset with numerous long setae, slope towards groove with 2 or 3 weak anterior and 2 or 3 posterior keels. **Tergites:** glabrous, but entirely covered by tiny pits. Tips of paratergites of midbody tergites projecting posteriorly (Fig. 6G). **Endotergum:** inner section without any setae or spines. Middle area with a single row of dense, round, cuticular impressions, distance between impressions slightly smaller than their diameter. Apically, 3–4 dense rows of short marginal bristles, the longest just protruding up to half of the distance to tergal margin. Bristles not smooth, but with numerous small spicules. **Anal shield:** well-rounded, surface completely covered by tiny setae each standing in a tiny pit. Underside with a single, black locking carina, located close to last laterotergite. Locking carinae of similar size to those of tergites. **Legs:** leg-pair 1 with 2 or 3 ventral spines, leg-pair 2 with 3 or 4, leg-pair 3 with 6. First two leg-pairs without an apical spine. Leg-pairs 4–21 with 9 or 10 ventral spines and one dorso-apical spine. In leg 9 femur 1.6 times, tarsus 3.7 times longer than wide (Fig. 20B). Femur extended mesally into a dentate margin featuring 12–14 teeth. All podomeres densely setose. Coxa with a well rounded process. Coxa process absent at first leg (Fig. 20A) and sharply projecting at second (Figs 20C; 21A).

**Female sexual characters:** Vulva of gravid female large, covering mesal 1/2 of coxa, extending mesally to anterior half of prefemur (Fig. 20C). Operculum rounded, mesal margin projecting into a well-rounded lobe 1/3 as high as remaining operculum. **Subanal plate:** large, high, broadly rounded triangular. Apex deeply recessed.

**Male sexual characters:** gonopore covered with a single, undivided, circular, sclerotized plate (Fig. 21A). **Anterior telopods** (Figs 21B–D): consisting of 4 telopoditomers above syncoxite, but telopoditomere 3 and 4 only divided by thin suture. Telopoditomere 1 slightly wider than long. Telopoditomere 2 large, as long as first, almost as long as telopoditomere 3 and 4 combined. Process of telopoditomere 2 located posteriorly, not visible in anterior view. Process of telopoditomere 2 wide, projecting to base of telopoditomere 4, apically with a well-rounded tip. Telopoditomere 3 cylindrical, straight, slightly smaller than telopoditomere 4. Telopoditomere 4 cylindrical, well-rounded, posterior side with two sclerotized spots. Telopoditomers 1–4 in anterior view covered with long setae. In posterior view all telopoditomers with fewer setae. **Posterior telopods** (Figs 22E, F): telopoditomere 1 rectangular, as long as wide. Immobile finger (process of telopoditomere 2) as long as movable finger, consisting of telopoditomers 3 and 4. Immobile finger with a characteristic, distally swollen apex. Apex expanding more towards movable finger than towards mesal margin, well rounded. Apex almost twice as wide as base. Telopoditomere 3 rectangular, twice as long as wide, towards immovable finger with a triangular expansion. Telopoditomere 4 reaching 2/3 of length of telopoditomere 3, slenderer, only weakly tapering but tip bent backwards into acute hook, very slightly curved towards immovable finger. Inner margin with two spines towards immovable finger. Telopoditomere 1 at both sides covered by setae. Telopoditomers 2 and 3 in anterior view covered by long setae, in posterior view mainly with marginal setae. Telopoditomere 4 glabrous.

**Derivatio nominis:** nigrum, noun in apposition, after the, for a member of *Sphaerobelum*, unique black colour of the legs, head, collum, antenna and part of the tergites.

### *Sphaerobelum splendidum* new species

Figures 6H, 9D, 22.

**Material examined:** 1 M holotype (SMF) from Laos, Bolikhamsay Province, Lak Sao (1) (N18°11'09.0", 104°53'55.0"E), 500 m; cave entrance, rocks, vegetation, leg. 8.XI.2009, at day, by hand, P. Jäger & S. Bayer.

**Diagnosis:** *S. splendidum* n. sp. belongs to a group of *Sphaerobelum* species in which the mesal margin of the femur is unmodified (Fig. 22B). *S. splendidum* n. sp. shares only with *S. hirsutum*, *S. clavigerum*, *S. nigrum* n. sp. and *S. schwendingeri* n. sp. the presence of a "hook" at telopoditomere 4 of the posterior telopods (Figs 22G, H). *S. splendidum* n. sp. differs from *S. hirsutum* in the presence of glabrous tergites, from *S. clavigerum* in the presence of a short locking carina on the anal shield. Differs from *S. nigrum* n. sp. in the presence of a cylindrical antennomere 6, the presence of only 5–7 ventral spines on the tarsi (8–10 ventral spines in the aother species) (Fig. 22B), and the presence of a strongly curved telopoditomere 4 of the posterior telopod, all characters only shared with *S. laoticum* n. sp. and *S. schwendingeri* n. sp. *S. splendidum* n. sp. differs from both in the following characters: Anterior telopod, telopoditomer 3 and 4 clearly separated (Figs 22D–F) (separation only partly visible in *S. laoticum* n. sp. and *S. schwendingeri* n. sp.), antennae and legs brown (both red in *S. laoticum* n. sp. and *S. schwendingeri* n. sp.).

**Description: Measurements:** Body length 21.4 mm. Width, of thoracic shield = 11.3 mm (= broadest). Height, of thoracic shield = 5.9 mm (= highest). **Coloration:** Head and collum chestnut brown. Tergites black olive green, posterior tergite margin light brown (Fig. 6H). Antennae and legs dirty brown.

**Head:** with 40–50 ocelli. Antennae extending posteriorly to leg 5. Size of antennomeres 1=2=3=4=5<6, 6th apically widened, not flat. Apical disc carrying 49/46 apical cones. Antennomere 1–5 with only few setae. Organ of Tömösváry located inside antennal groove. **Gnathochilarium:** usual for the order, sensory cones located in clusters. **Mandibles:** not investigated.

**First stigmatic plate:** small, well-rounded, inconspicuous (Fig. 22A). **Laterotergites:** 1 and 2 with a short, but sharp, spine-like projection. **Collum:** only short setae at margin.

**Thoracic shield:** Shallow grooves with few setae, surface glabrous. Margin towards grooves with 2 anterior and 3 or 4 posterior keels. **Tergites:** shiny, polished, at high magnification chagrinated. Paratergite tips weakly projecting posteriorly (Fig. 6H). Tergite surface glabrous except for paratergite grooves. **Endotergum** (Fig. 9D): inner section without setae or spines. Single, sparse row of slightly elliptical large cuticular impressions, distance between impressions slightly larger than their diameter. Externally 2–3 rows of medium length marginal bristles, protruding at most up to tergite margin (Fig. 9D). **Legs:** leg-pair 1 with 2 ventral spines, leg pair 2 with 3, leg pair 3 with 4 or 5, leg pairs 4–21 with only 5–7. Apical spine present at tarsi 3–21. In leg 9, femur 1.6 times, tarsus 3.3 times longer than wide (Fig. 22B). Coxae 1 and 2 without a coxal process (Figs 22A, C). **Anal shield:** well-rounded, glabrous, underside with a single very small, almost dot-like, locking carina.

**Male sexual characters:** Male gonopore large, covered by small, inconspicuous plate (Fig. 22C). **Anterior telopods** (Figs 22D–F): telopoditomere 1 rectangular, as long as wide. Telopoditomere 2 large, as long as telopoditomer 3 and 4 combined. Process of telopoditomere 2 located posteriorly and laterally, visible in anterior view. Process of telopoditomere 2 slender, projecting almost as high as apical part of telopoditomere 4, apical part well-rounded. Telopoditomere 3 as long as wide, almost twice as long as telopoditomere 4, inconspicuous. telopoditomere 3 and 4 fused in posterior view, divided by a suture in anterior and lateral views. Telopoditomere 4 well-rounded, tapering apically. Posterior aspect with one black sclerotized spot and 2 spines. All podomeres apically covered with long setae. **Posterior telopods** (Figs 22G, H): telopoditomere 1 elongated, twice as long as wide. Immobile finger (process of telopoditomere 2) as long as movable finger, consisting of telopoditomer 3 and 4. Immobile finger with a characteristic, distally swollen apex, massively swollen and curved towards movable finger. Apically broader than base. Telopoditomere 3 elongated, towards immobile finger at midpoint with a triangular extension carrying two large spines. Telopoditomere 4 tapering, apically strongly curved towards immobile finger, with thinly projecting apex. At inner margin with a large spine at midpoint and 1 or 2 smaller spines apically. Entire telopoditomere 1 and 2 at both sides covered with long setae, except for the immobile finger. Telopoditomere 3 only baso-laterally with a few setae, remaining part as well as telopoditomere 4 glabrous.

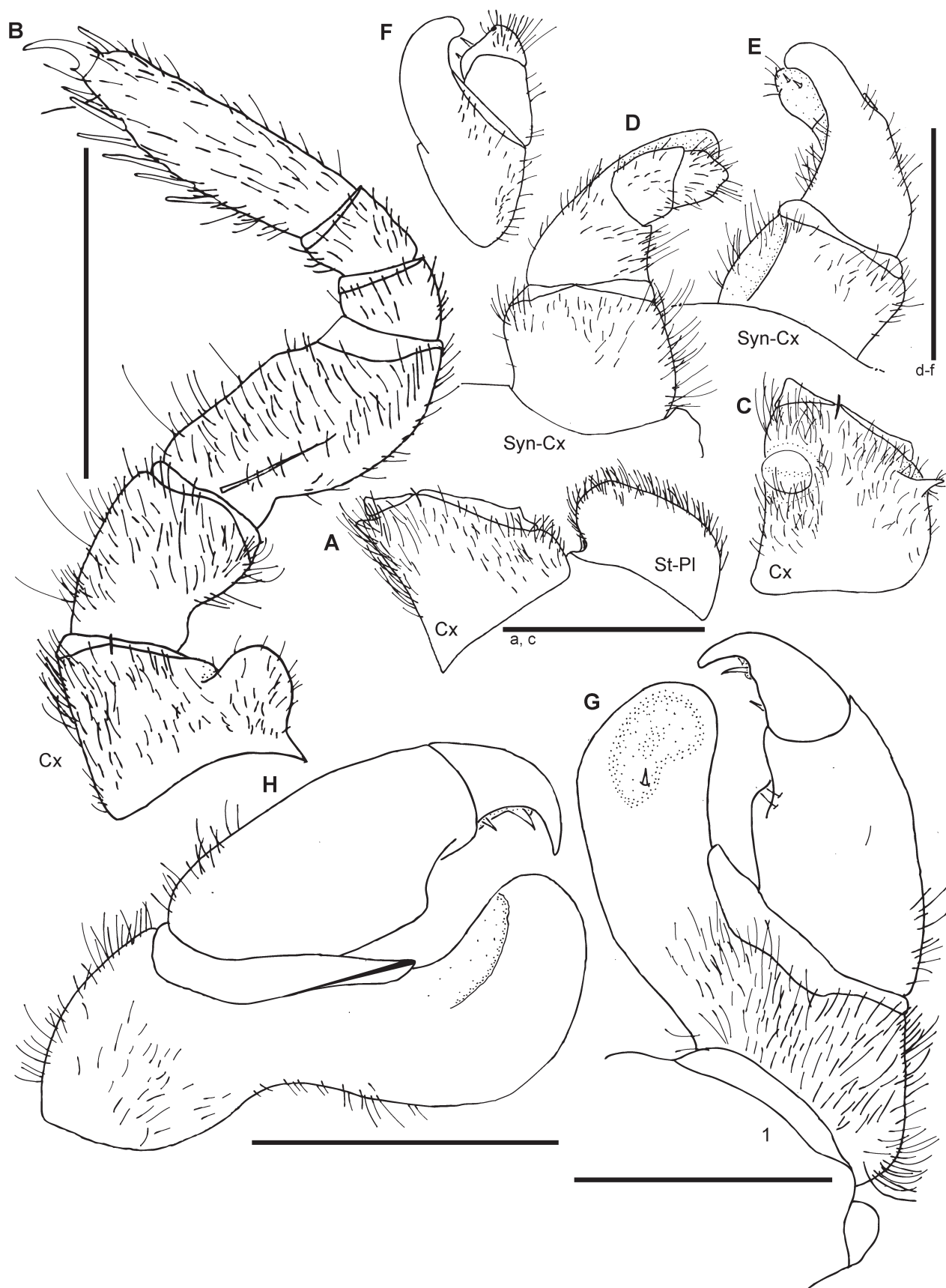
**Derivatio nominis:** splendidum, noun in apposition, based on the shiny appearance of this species.

### *Sphaerobelum laoticum* new species

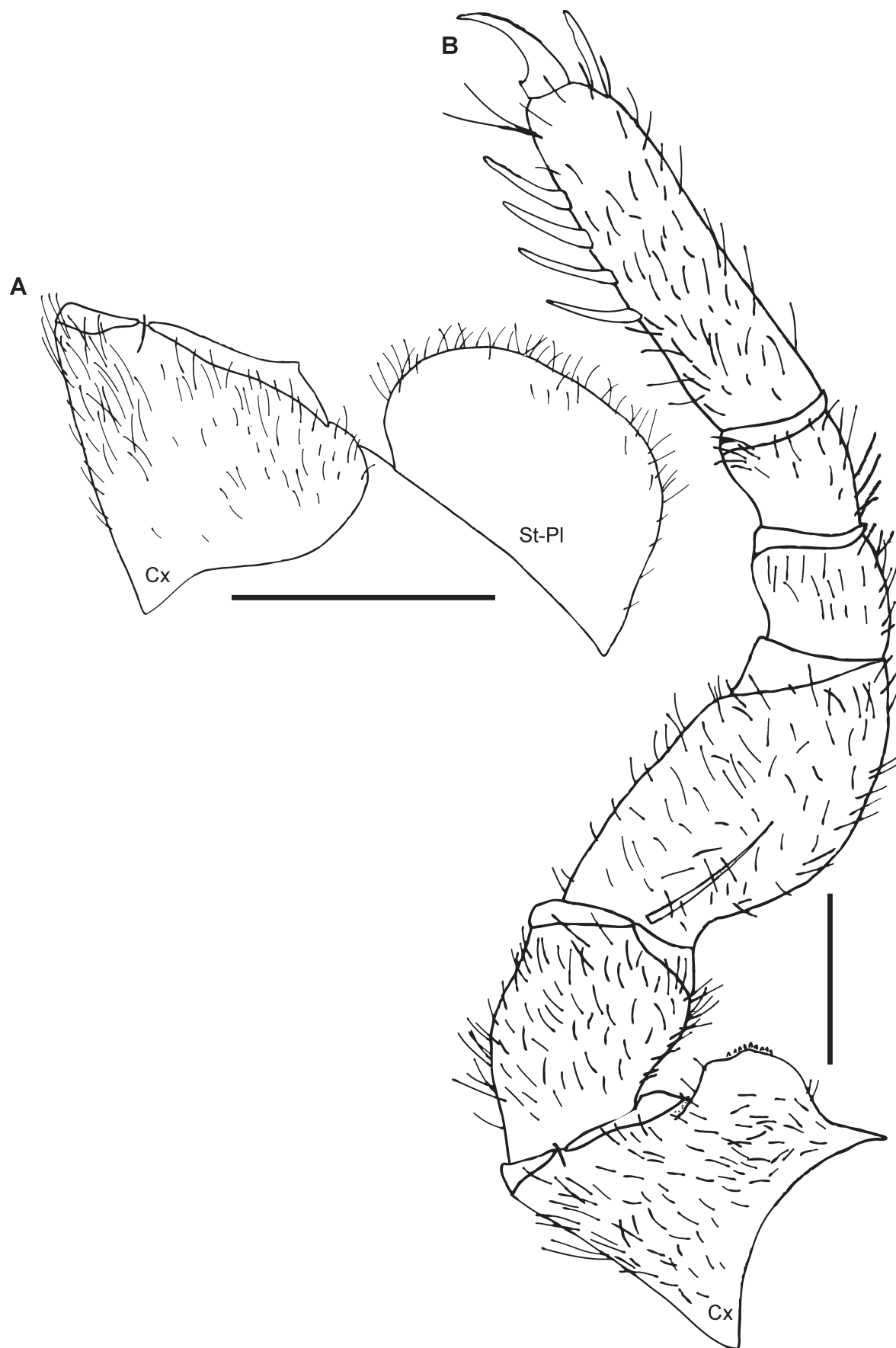
Figures 6I, 23, 24.

**Material examined:** Type material. 1 M holotype (SMF) from Laos, Vientiane Province, Vang Vieng, W. of Nam Song (N18°55'46.86", 102°20'56.82"E), 324 m, Tham Nam Or Khem, in cave, leg. by hand, 28.VII.2014, P. Jäger & S. Münnich.

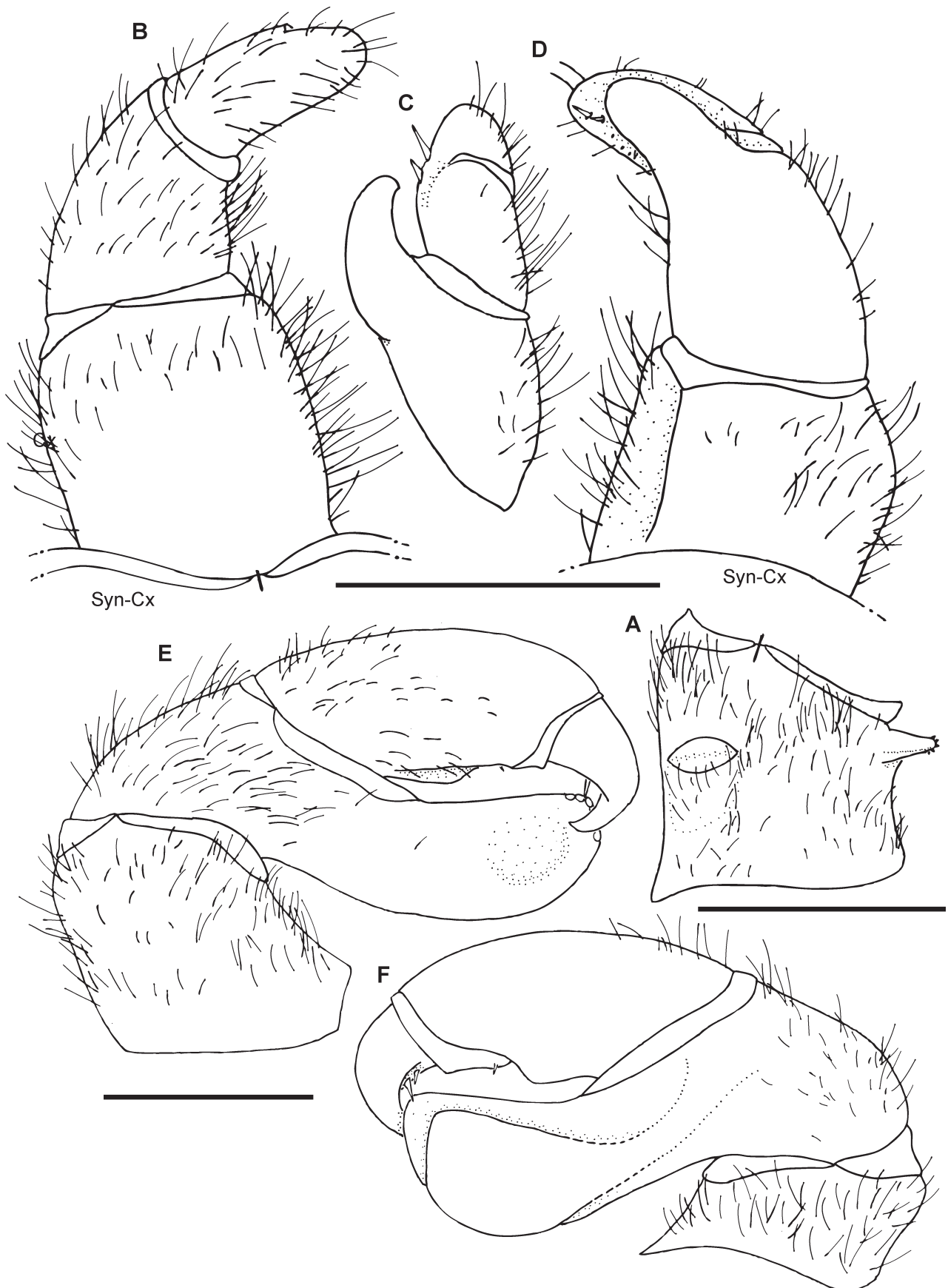




**FIGURE 22.** *Sphaerobelum splendidum* n. sp., holotype (SMF); **A:** coxa of first left leg with first stigmatic plate; **B:** 9th left leg; **C:** coxa of second left leg with gonopore; **D:** left anterior telopod, anterior view; **E:** left anterior telopod, posterior view; **F:** left anterior telopod, lateral view; **G:** right posterior telopod, anterior view; **H:** right posterior telopod, posterior view. Abbreviations: Cx = coxa; St-Pl = stigmatic plate; Syn-Cx = syncoxite. Scale bars = 1 mm.



**FIGURE 23.** *Sphaerobelum laoticum* n. sp., holotype (SMF); **A:** coxa of first left leg with first stigmatic plate; **B:** 9th left leg. Abbreviations: **Cx** = coxa; **St-Pl** = stigmatic plate. Scale bars = 1 mm.



**FIGURE 24.** *Sphaerobelum laoticum* n. sp., holotype (SMF); **A:** coxa of second left leg with gonopore; **B:** left anterior telopod, anterior view; **C:** left anterior telopod, posterior view; **D:** left anterior telopod, lateral view; **E:** left posterior telopod, anterior view; **F:** left posterior telopod, posterior view. Abbreviations: Cx = coxa; Syn-Cx = syncoxite. Scale bars = 1 mm.

**Other material examined:** 1 imm. M (SMF) from Laos, Vientiane Province, Van Vieng, Ban Sok Say (N19°1'20.30", 102°26'54.11"E), 295 m, in vegetation, leg. by hand, P. Jäger & S. Packheiser, 23.VII.2018. 1 imm. F (SMF) from Laos, Vientiane Province, Van Vieng, N of Ban Phoxay, Tham Hoi and Tham Loup, in cave (N19°02.350', 102°25.423'E), 256 m, leg. by hand, P. Jäger & S. Packheiser, 23.VII.2018.

**Diagnosis:** *S. laoticum* n. sp. belongs to a group of *Sphaerobelum* species in which the mesal margin of the femur is unmodified (Fig. 23B). *S. laoticum* n. sp. shares only with *S. hirsutum*, *S. clavigerum*, *S. nigrum* n. sp., *S. splendidum* n. sp. and *S. schwendingeri* n. sp. the presence of a "hook" at telopoditomere 4 of the posterior telopods (Figs 24E, F). *S. laoticum* n. sp. differs from *S. hirsutum* in the presence of glabrous tergites, from *S. clavigerum* in the presence of a short locking carina on the anal shield. It differs from *S. nigrum* n. sp. in the presence of a cylindrical antennomere 6, the presence of only 5–7 ventral spines on the tarsi (8–10 in the other species) (Fig. 23B), and the presence of a strongly curved telopoditomere 4 of the posterior telopod, all characters only shared with *S. splendidum* n. sp. and *S. schwendingeri* n. sp. For a differentiation of *S. laoticum* n. sp. with *S. splendidum* n. sp. see above. *S. laoticum* n. sp. differs from *S. schwendingeri* n. sp., which occurs almost in sympatry, in a genetic distance of 13.6% in the COI gene, the process of telopoditomere 2 of the anterior telopods projecting as high as basal 1/3 (3/4 in *S. schwendingeri* n. sp.) of telopoditomere 3+4 (Fig. 22F); anal shield with a single short locking carinae (absent in *S. schwendingeri* n. sp.); palpi of gnathochilarium, sensory cones located in single field (in several clusters in *S. schwendingeri* n. sp.).

**Description:** Based on male holotype

**Measurements:** body length 24.4 mm. Width, of thoracic shield = 12.7 mm (= widest). Height, of thoracic shield = 7.4 mm (= highest). **Coloration:** Head and collum black. Tergites black (fading to brown in longer preserved specimens), paratergite depressions olive green (Fig. 6I). Antennae and legs red.

**Head:** with ca. 65 ocelli. Antennae extending posteriorly to leg 5. Size of antennomeres 1=2=3=4=5<<6, 6th apically widened. Apical disc carrying 81/86 apical cones. Antennomere 1–5 with only few setae. Organ of Tömösváry located in antennal groove. **Gnathochilarium:** with the usual shape for the order, sensory cones located in single field. **Mandibles:** not investigated.

**First stigmatic plate:** small, well-rounded, inconspicuous, slightly curved towards coxa (Fig. 23A). **Laterotergites:** 1 and 2 with a short, well-rounded projection. **Collum:** glabrous only short setae at margin. **Thoracic shield:** Shallow grooves with few setae, surface glabrous. Margin towards grooves with three or four weak anterior, and 2 or 3 posterior crests. **Tergites:** shiny, polished, no pits or setae present in posterior 2/3. Anterior 1/3, which is mainly visible when the specimen is rolled up, with longer setae providing a golden sheen. Paratergite tips weakly projecting posteriorly (Fig. 6I). **Endotergum:** inner section without any setae or spines. Middle area with a single row of sparse elliptical, cuticular impressions, distance between impressions larger than their diameter. Apically 3 dense rows of short marginal bristles, the longest just protruding up to tergal margin. Bristles not smooth, but with numerous small spicules. **Anal shield:** well-rounded, covered with numerous tiny setae, underside with a single very small, almost dot-like, locking carina. **Legs:** leg-pair 1 with 2 ventral spines, leg-pair 2 with 4, leg-pair 3 with 6, leg-pairs 4–21 with only 4–7. Apical spines at present tarsi 3–21. In leg 9, femur 1.6 times, tarsus 3.9 times longer than wide (Fig. 23B). Leg 1 without a coxal process (Fig. 23A), leg 2 with a sharp coxal process (Fig. 24A), while the process is well-rounded in the following legs.

**Male sexual characters:** male gonopore large, covered by small, inconspicuous plate (Fig. 24A). **Anterior telopods** (Figs 24B–D): consisting of three telopoditomere above syncoxite. Last telopoditomere divided by a suture still visible in lateral view. Telopoditomere 1 rectangular, slightly longer than wide. Telopoditomere 2 large, as long as telopoditomere 3. Process of telopoditomere 2 located posteriorly, not visible in anterior view. Process of telopoditomere 2 wide, projecting to half of telopoditomere 3, slightly curved, apically with a sharp tip. Telopoditomere 3 massive, cylindrical, straight, apically slightly tapering. Posterior side with two large, triangular spines. In anterior view all telopoditomeres covered by long setae, in posterior view telopoditomeres 2 and 3 only with marginal setae. **Posterior telopods** (Figs 25E, F): telopoditomere 1 rectangular, slightly longer than wide. Immobile finger (process of telopoditomere 2) slightly shorter than movable finger, consisting of telopoditomeres 3 and 4. Immobile finger with a characteristic, distally swollen apex, slightly swollen. Apically broader than base, at tip in anterior view with a few large, crenulated teeth. Telopoditomere 3 elongated, towards immobile finger at midpoint with a triangular extension carrying a spines. Telopoditomere 4 tapering, anterior half strongly curved 90° towards immobile finger, which it overlaps. At inner margin with two larger spines. Entire telopoditomeres 1 and 2 on both sides covered with long setae, except for the immobile finger. Telopoditomere 3 only basally in anterior view with setae, remaining part as well as telopoditomere 4 glabrous.



**Intraspecific variation:** *S. laoticum* **n. sp.** is the giant pill-millipede species from Laos with the most known localities (3, all in a 15 km radius, Fig. 5) and specimens. The specimens from the different localities show considerable intraspecific variation. The smaller, not fully mature specimens from Ban Sok Say and Tham Loup display one, sometimes two weak short locking carinae. These samples were collected recently and might require Nagoya permissions to be barcoded, so an analysis of the intraspecific variation between these populations was not possible.

**Remarks:** This species, only known from males, lives syntopically with two other *Sphaerobelum* species, one only known from females. *Sphaerobelum* sp. L10, and *S. schwendingeri* (Fig. 5, see below). Genetic barcoding data clearly reveals that the specimens, collected from a close-by location, are distinct species, differing in 15.9% (to *S. sp.* L10) or 13.6 % p-distance (to *S. schwendingeri* **n. sp.**) in the COI gene in the barcoding COI gene.

**Derivatio nominis:** laoticum, noun in apposition, after Laos, as this is the first *Sphaerobelum* known from this country.

### *Sphaerobelum schwendingeri* new species

Figure 25

**Material examined:** Type material. 1 M holotype (MHNG LT 10/03) from Laos, Vientiane Province, trail to Tham Pou Kham, W. of Vang Vieng (N18°55'32", 102°23'58"E), 240 m, secondary forest on limestone hill, leg. 7.IX.2010, P. Schwendinger. 1 M paratype (MHNG LT 10/03), same data as previous. 1 F paratype (SMF), from Laos, Vientiane Province, Vang Vieng, Tham Pou Kham, 260 m (N18°55.549', 102°23.734'E), outside cave, close to cave stream, at rocks, leg. by hand, 13.III.2007, P. Jäger & F. Steinmetz.

**Other material examined:** 1 M, 1 imm. F (SMF) from Laos, Vientiane Province, Van Vieng, across Nam Song, Tham Chang, in or in front of cave (N18°54.550', 102°26.527'E), 270 m, leg. by hand, P. Jäger & S. Packheiser, 22.VII.2018. 1 M (ZFMK MYR8103), same data as previous.

**Diagnosis:** *S. schwendingeri* **n. sp.** belongs to a group of *Sphaerobelum* species in which the mesal margin of the femur is unmodified (Fig. 25B). *S. schwendingeri* **n. sp.** shares only with *S. hirsutum*, *S. clavigerum*, *S. nigrum* **n. sp.**, *S. splendidum* **n. sp.** and *S. laoticum* **n. sp.** the presence of a "hook" at telopoditome 4 of the posterior telopods (Figs 25F, G). *S. schwendingeri* **n. sp.** differs from *S. hirsutum* in the presence of glabrous tergites, from *S. clavigerum* in the presence of a short locking carina on the anal shield. It differs from *S. nigrum* **n. sp.** in the presence of a cylindrical antennomere 6, the presence of 8–10 ventral spines on the tarsi (Fig. 25B), and the presence of a strongly curved telopoditome 4 of the posterior telopod, all characters only shared with *S. splendidum* **n. sp.** and *S. laoticum* **n. sp.** For a differentiation of *S. schwendingeri* **n. sp.** with *S. splendidum* **n. sp.** see above. For a differentiation to *S. laoticum* **n. sp.** see above.

**Description:** based on male holotype and paratypes of both sexes.

**Measurements:** holotype male: body length 27.3 mm. Width, of thoracic shield = 13.3 mm (= widest). Height, of thoracic shield = 7.4 mm high (= highest). Female: Body length: broken and rolled up, ca. 37 mm. Width, of thoracic shield = 18 mm (unclear of broadest, broken). **Coloration:** in preserved specimens tergites black, posterior third olive. Head and collum black, anterior half of head green. Antennae and legs orange-red.

**Head:** Eyes with ca. 70 ocelli. Last antennomere thickened. Apical disc with 73/71 apical cones (male), or 36/37 (female). All antennomeres covered by long setae. Organ of Tömösváry located inside antennal groove.

**Gnathochilarium:** structure typical of the order. Palpi sensory cones located in several clusters. **Mandibles:** not dissected.

**Stigmatic plates:** first stigmatic plate widely rounded, apex well-rounded, slightly curved towards coxa 1 (Fig. 25A). **Laterotergites:** laterotergite 1 and 2 slightly elongated into a short, broad process. **Collum:** with glabrous surface, margins with few isolated setae. **Thoracic shield:** surface glabrous, but covered with small pits like tergites, setae only in grooves. Shallow grooves beset with numerous long setae, slope towards groove without keels. **Tergites:** glabrous, shiny. Anterior third with a few setae only visible when the specimen is rolled up, producing a golden sheen. Tips of paratergites of midbody tergites projecting posteriorly. **Endotergum:** inner section without any setae or spines. Middle area with a single row of sparse elliptical, cuticular impressions, distance between impressions larger than their diameter. Apically 3–4 dense rows of short marginal bristles, the longest just protruding up to half of length to tergal margin. Bristles not smooth, but with numerous small spicules.

**Anal shield:** sexually dimorphic, in female slightly flattened, in male weakly bell-shaped. Glabrous. Underside without locking carinae. **Legs:** leg-pair 1 with 2 ventral spines, leg-pair 2 with 6, leg-pair 3 with 6. First two leg-pairs without an apical spine. Leg-pairs 4–21 with 6–8 ventral spines and one dorso-apical spine. In leg 9 femur 1.7 times, tarsus 3.8 times longer than wide (Fig. 25B). All podomeres densely setose. Coxa with a well rounded process. Coxa process absent at first leg (Fig. 25A) and sharp-edged at second (Fig. 25C).

**Female sexual characters:** Vulva large, covering mesal 2/3 of coxa, extending mesally to anterior third of prefemur (Fig. 25C). Operculum rounded, central part recessed, mesal margin broadly projecting into a sharp-edged triangle slightly as higher than remaining operculum. **Subanal plate:** not examined.

**Male sexual characters:** gonopore large, covered by small, inconspicuous plate. **Anterior telopods** (Figs 25D, E): Consisting of three telopoditomere above syncoxite. Last telopoditomeres completely fused. Telopoditomere 1 rectangular, slightly longer than wide. Telopoditomere 2 large, as long as telopoditomere 3. Process of telopoditomere 2 located posteriorly, apex visible in anterior view. Process of telopoditomere 2 wide, projecting to length of telopoditomere 3, strongly curved, apically with a well-rounded tip. Telopoditomere 3 massive, cylindrical, straight, apically slightly tapering. Posterior side with three large spines. In anterior view all telopoditomeres covered by long setae, in posterior view telopoditomeres 2 and 3 only with marginal setae.

**Posterior telopods** (Figs 25F, G): telopoditomere 1 rectangular, slightly longer than wide. Immovable finger (process of telopoditomere 2) shorter than movable finger, consisting of telopoditomeres 3 and 4. Immovable finger with a spine in anterior view, a characteristic, distally swollen apex, slightly swollen. Apically broader than base, at tip in anterior view with a few large, crenulated teeth. Telopoditomere 3 elongated, at midpoint with a triangular extension carrying a spine towards immovable finger. Telopoditomere 4 tapering, anterior half strongly curved 90° towards immovable finger, which it overlaps. At inner margin with two larger spines. Entire telopoditomere 1 at both sides covered with long setae. Telopoditomere 2 anterior side completely covered by setae except for tip of immovable finger, posterior side glabrous except for lateral margin. Telopoditomere 3 only basally in anterior view with setae, remaining part, as well as telopoditomere 4 glabrous.

**Derivatio nominis:** schwendingeri, noun in apposition, after the Arachnologist Peter Schwendinger, great collector of arthropods in Southeast Asia.

### **Species incertae sedis known solely from female specimens:**

The following specimens can be easily distinguished from one another as well as from the 11 species described above by morphological characters as well as barcoding data. Two species, *S. sp. L10*, and *S. sp. L07* are assigned to the genus *Sphaerobelum*, while the genus assignment of Zephroniidae sp. L04b remains to be resolved. The species are currently not named, as no male specimens are available (male characteristics provide the basis of species taxonomy of the group). The barcoding data and the detailed morphological descriptions may provide enough data to assign these specimens to species once additional material from Laos or surrounding countries becomes available.

### ***Sphaerobelum* sp. L10**

**Material examined:** 1 F (SMF) from Laos, Vientiane Province, Vang Vieng, W. of Nam Song (N18°55'46.86", 102°20'56.82"E), 324 m, Tham Nam Or Khem, in front of cave; leg. by hand, 28.VII.2014, P. Jäger & S. Münnich.

**Unique characters:** Brown species, tergites covered by pits. Anal shield without locking carinae. Legs unmodified with surprisingly few ventral spines (Fig. 25B). Operculum of vulva on protruding up to basal 1/5 of prefemur, mesally extended (Fig. 25C). Coxa 2 with a weakly developed process (Fig. 26C).

**Description: Measurements:** Body length ca 24.7 mm. Width, of thoracic shield = 14.6 mm. Height, of thoracic shield = 8.2 mm. **Coloration:** in preserved specimen light brown. Head and collum slightly darker brown. Antennae and legs light brown.

**Head:** Eyes with ca. 55 ocelli. Last antennomere thickened. Apical disc with 38/39 apical cones. All antennomeres covered by long setae. Organ of Tömösváry located inside antennal groove. **Gnathochilarium:** structure typical of the order. Palpi sensory cones in several clusters. **Mandibles:** not dissected.

**Stigmatic plates:** first stigmatic plate widely rounded, apex well-rounded, slightly curved towards coxa 1 (Fig.

26A). **Laterotergites**: laterotergite 1 and 2 slightly elongated into a short, broad process. **Collum**: with glabrous surface, margins with few isolated setae. **Thoracic shield**: surface glabrous, but covered with small pits like tergites, setae only in grooves. Shallow grooves beset with numerous long setae, slope towards groove without keels. **Tergites**: glabrous, but entirely covered by tiny pits. Tips of paratergites of midbody tergites projecting posteriorly. **Anal shield**: slightly flattened. Underside without locking carinae. **Legs**: leg-pair 1 with 2 ventral spines, leg-pair 2 with 3 or 4, leg-pair 3 with 5. First two leg-pairs without an apical spine. Leg-pairs 4–21 with 6 ventral spines and one dorso-apical spine. In leg 9 femur 1.8 times, tarsus 4.6 times longer than wide (Fig. 26B). All podomeres densely setose. Coxa with a well rounded process. Coxa process absent at first leg (Fig. 26A) and weakly developed at second (Fig. 26C).

**Female sexual characters**: Vulva small, covering mesal half of coxa, extending mesally to anterior fifth of prefemur (Fig. 26C). Operculum rounded, mesal margin strongly projecting into a well-rounded lobe twice as high as remaining operculum. **Subanal plate**: large and wide, undivided, central margin slightly recessed. Densely setose (Fig. 26D).

### *Sphaerobelum* sp. L07

**Material examined**: 1 F (ZMUC00040261) from Laos; Khammouane Province, Ban Khounkham [Khun Kham] (Nahin), 300 m; disturbed primary lowland evergreen forest, flight intercept trap (N18°13.027', 104°30.880'E), leg. 4–18.VI.2008, A. Solodovnikov & J. Pedersen.

**Unique characters**: Medium sized species, tergites brown with a darker posterior margin. Antennae and legs conspicuously yellow. Tergites covered by pits. Anal shield with single, long locking carinae. First laterotergite extending posteriorly in a long, pointed process. Legs unmodified with a high number of ventral spines (10–12, Fig. 27B). Operculum of vulva unique for species from Laos, protruding completely up to basal 2/3 of prefemur with one triangular, widely rounded tip (Fig. 27C). Coxa 2 lacking a process (Fig. 27C).

**Description: Measurements**: Body length ca 24.6 mm. Width, of thoracic shield = 13.5 mm. Height, of thoracic shield = 7.9 mm. **Coloration**: in preserved specimens orange to brown with darker posterior margin. Head and collum same colour as tergites. Antennae and legs yellow.

**Head**: Eyes with ca. 55 ocelli. Last antennomere thickened. Apical disc with 31/27 apical cones. All antennomeres covered by long setae. Organ of Tömösváry located inside antennal groove. **Gnathochilarium**: structure typical of the order. Palpi sensory cones in several clusters. **Mandibles**: not dissected.

**Stigmatic plates**: first stigmatic plate widely rounded, apex well-rounded, slightly curved towards coxa 1 (Fig. 27A). **Laterotergites**: laterotergite 1 strongly elongated into a long, sharp process. Laterotergite 2 slightly elongated into a pointed process. **Collum**: with glabrous surface, margins with few isolated setae. **Thoracic shield**: surface glabrous, setae only in grooves. Shallow grooves beset with numerous long setae, slope towards groove without keels. **Tergites**: glabrous. Tips of paratergites of midbody tergites projecting posteriorly. **Anal shield**: well rounded. Underside without locking carinae. **Legs**: leg-pair 1 with 2 ventral spines, leg-pair 2 with 5, leg-pair 3 with 7. First two leg-pairs without an apical spine. Leg-pairs 4–21 with 10–12 ventral spines and one dorso-apical spine. In leg 9 femur 1.6 times, tarsus 5 times longer than wide (Fig. 27B). All podomeres densely setose. Coxa with a well rounded process. Coxa process absent at first leg (Fig. 27A) and weakly developed at second (Fig. 27C).

**Female sexual characters**: Vulva large, covering mesal 3/4 of coxa, extending mesally to basal 2/3 of prefemur (Fig. 27C). Operculum unique for Laotian millipedes, rounded, elongated into a well-rounded, wide triangle. **Subanal plate**: large and wide, undivided, central margin slightly recessed. Densely setose (Fig. 27D).

### Unknown genus, Zephroniidae sp. L04b

**Material examined**: 1 F (ZMUC00040262) from Laos, Champasak Province, Bolaven plateau, Ban Houayteuay, 1200 m (N15°4.655', 106°16.848'E), disturbed montane forest, leg. 10.XII.2007, by hand, S. Tarasov.

**Unique characters**: large species, tergites yellow-brown with a darker posterior margin. Antennae and legs conspicuously orange. Tergites covered by numerous short setae. Anal shield without locking carinae. Thoracic

shield with 7 well-developed crests. First laterotergite extending posteriorly in a short, pointed process. Legs with modified mesal margin at prefemur and femur, with 8–10 ventral spines (Fig. 28B). Operculum rounded, mesal margin strongly projecting into a well-rounded lobe twice as high as remaining operculum (Fig. 28C). Coxa 2 lacking a process (Fig. 28C). Subanal plate divided into two (Fig. 28D).

**Description: Measurements:** Body length ca 34.1 mm. Width, of thoracic shield = 15.7 mm. Height, of thoracic shield = 8.9 mm. **Coloration:** in preserved specimens yellow-brown with darker posterior margin. Head and collum same colour as tergites. Antennae and legs orange.

**Head:** Eyes with ca. 100 ocelli. Last antennomere thickened. Apical disc with 23/26 apical cones. All antennomeres covered by long setae. Organ of Tömösváry located inside antennal groove. **Gnathochilarium:** structure typical of the order. Palpi sensory cones located in single field. **Mandibles:** not dissected.

**Stigmatic plates:** first stigmatic plate widely rounded, apex well-rounded, not curved towards coxa 1 (Fig. 28A). **Laterotergites:** laterotergite 1 slightly elongated into a short, sharp process. **Collum:** with glabrous surface, margins with few isolated setae. **Thoracic shield:** surface glabrous, setae only in grooves. Shallow grooves beset with numerous long setae, slope towards groove with 7 well-developed keels. **Tergites:** completely covered by numerous small setae. Tips of paratergites of midbody tergites projecting posteriorly. **Anal shield:** well rounded, completely covered by tiny pits with a small setae each. Underside without locking carinae. **Legs:** leg-pair 1 with 3 ventral spines, leg-pair 2 with 5, leg-pair 3 with 6. First two leg-pairs without an apical spine. Leg-pairs 4–21 with 8–10 ventral spines and one dorso-apical spine. In leg 9 femur 1.2 times, tarsus 4.3 times longer than wide (Fig. 28B). All podomeres densely setose. Prefemur at apico-mesal margin with a sharp projection. Mesal margin of femur extended, tessellated with up to 7 well-rounded extensions. Coxa with a well rounded process. Coxa process absent at first leg (Fig. 28A) and second (Fig. 28C).

**Female sexual characters:** Vulva large, covering mesal 2/3 of coxa, extending mesally to anterior third of prefemur (Fig. 28C). Operculum rounded, mesal margin strongly projecting into a well-rounded lobe twice as high as remaining operculum. **Subanal plate:** large and wide, divided into two parts by a mesal suture. Densely setose (Fig. 28D).

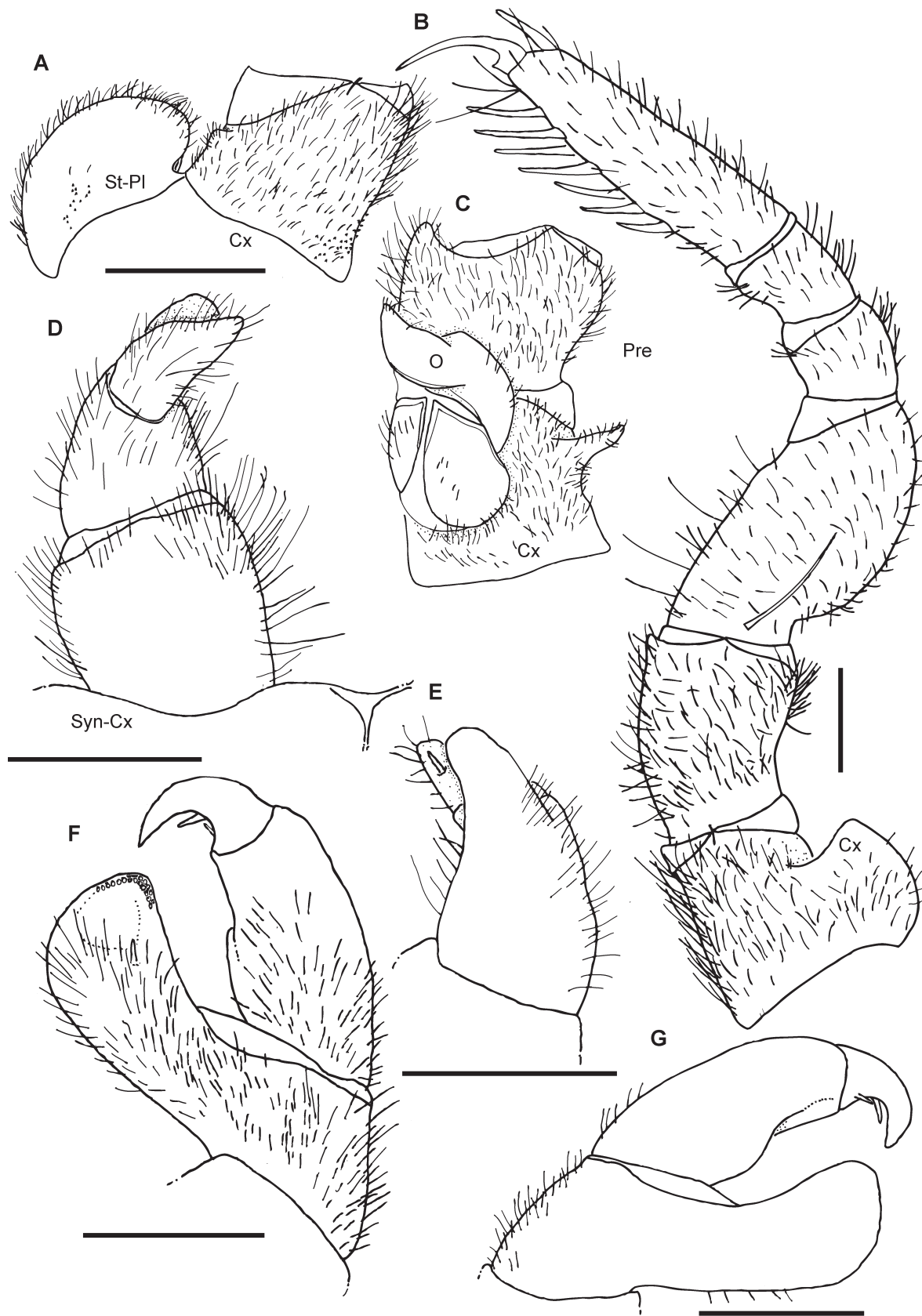
**Remarks:** No DNA barcode is available for Zephroniidae sp. L04b

## Discussion

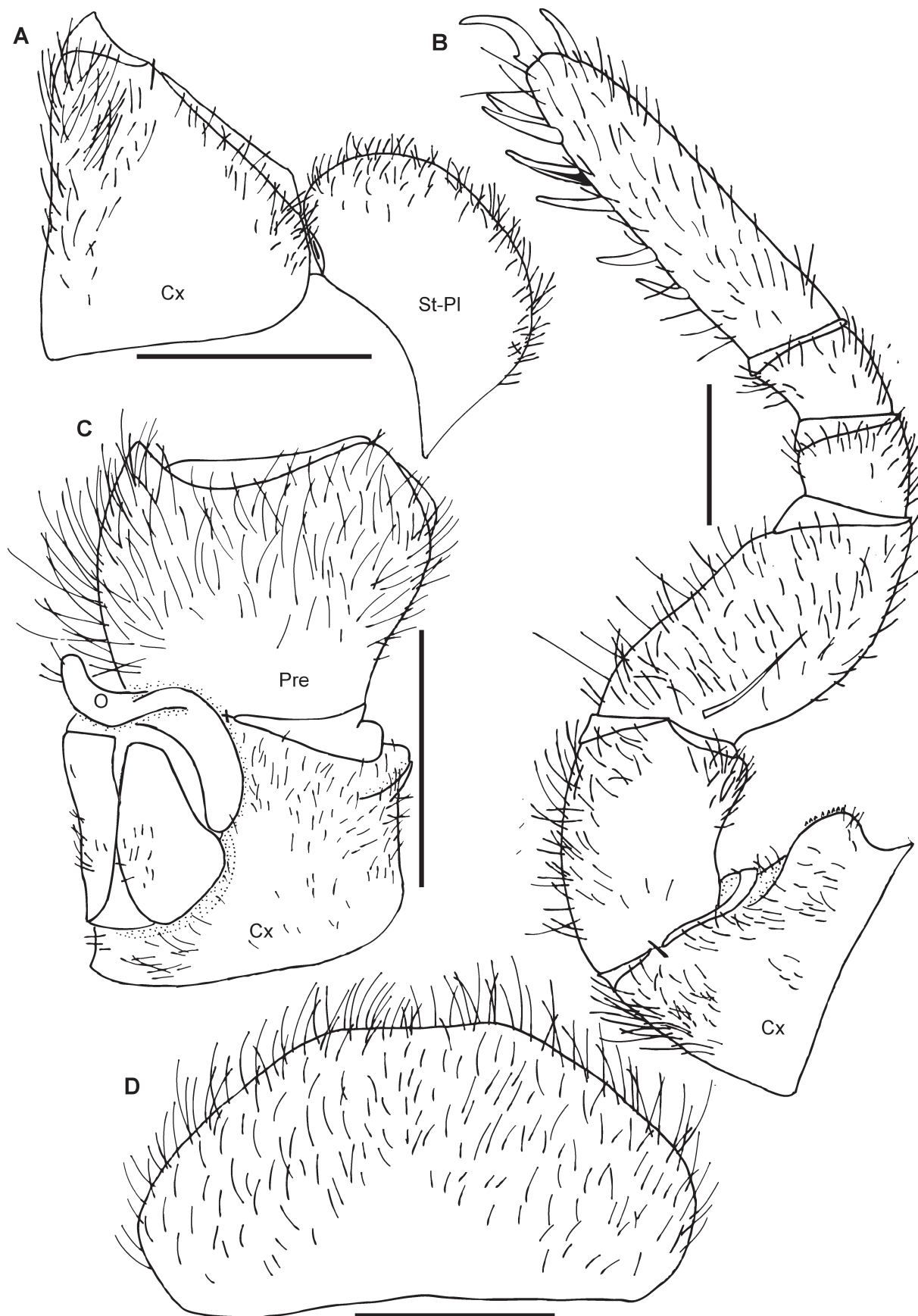
Based on the fact that giant pill-millipedes can be found in every part of Laos (Figs 2, 5), and that a total of 31-collected specimens yielded 14 different giant pill-millipede species (with two records of two species occurring in direct syntopy) it is safe to say that at this point that the Sphaerotheriida fauna of Laos is still very incompletely known. Despite evidence of a more cryptic lifestyle (dirt attached to tergites) of *Sphaerobelum* species, perhaps reflected in the much lower number of species described from *Sphaerobelum* compared to *Zephronia* (7 vs. 41 before this study), it is remarkable that ten out of eleven Sphaerotheriida species from Laos belong to the genus *Sphaerobelum*. Although the genus *Zephronia* is dominant and diverse elsewhere in Vietnam, Myanmar and NE India (Wesener 2016a; Semenyuk *et al.* 2018), only a single species is known from Laos, Cambodia and Thailand (Enghoff 2005; Likhitrakarn *et al.* 2015c).

Genetic barcoding proved to be especially useful in this taxonomic study of millipedes for placing species only represented by females in the correct genus, in addition to correctly associating females to males. The large genetic distances (mean >9%, in most cases >15%) between the Laotian species of both *Sphaerobelum* and *Zephronia*, with their closest relatives—in some cases not found in Laos but in other SE Asian countries—is evidence of an ancient evolutionary and biogeographical history that led to the current millipede diversity of the country of Laos. A more detailed study of their evolutionary diversification remains hampered by the incomplete knowledge of the millipede alpha-diversity and the distribution of species not only in Laos, but also in most surrounding countries. Barcodes also revealed that the genera of the Zephroniidae, despite clear progress in recent revisions of several genera (Mauriès 2001; Golovatch *et al.* 2012; Wesener 2016b), are not as well defined as in other millipede groups (e.g. Wesener *et al.* 2010; Moritz & Wesener 2017), with evidence that some genera might not be entirely monophyletic.

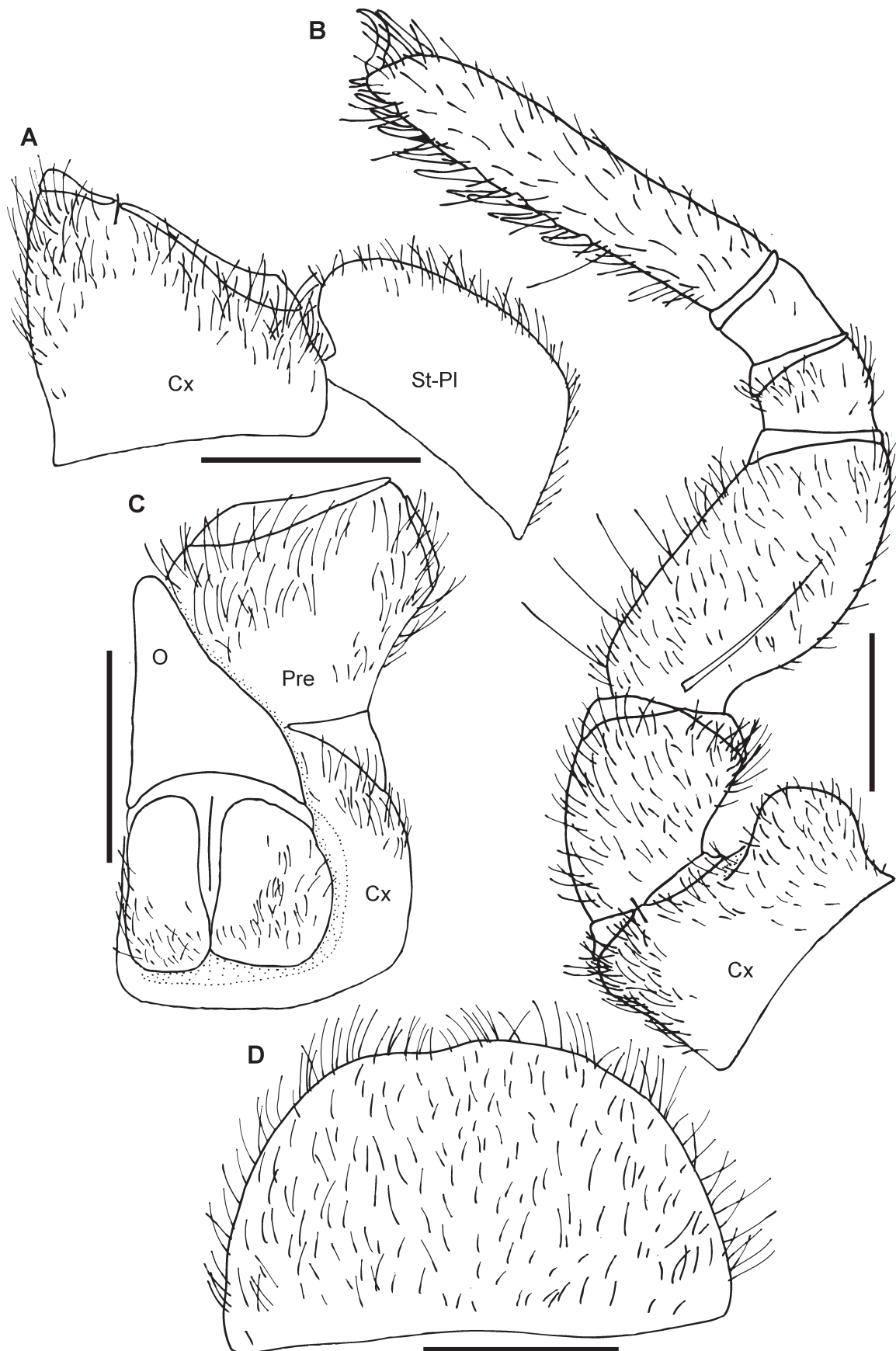




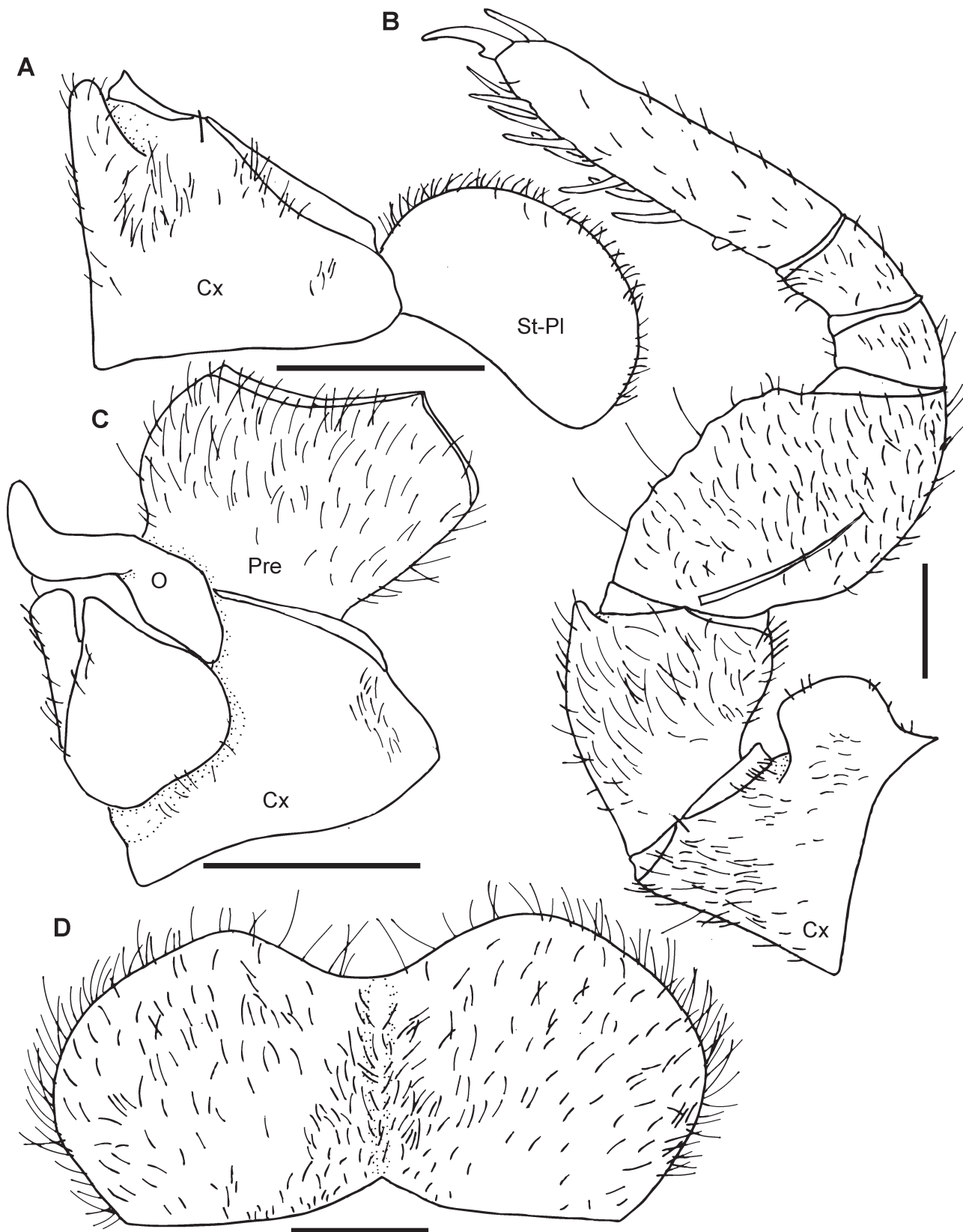
**FIGURE 25.** *Sphaerobelum schwendingeri* n. sp. A–C female paratype (ZMUC), D–G male holotype (MHNG). A: coxa of first right leg with first stigmatic plate; B: 9th left leg; C: coxa and prefemur of second leg with vulva; D: left anterior telopod, anterior view; E: left anterior telopod, posterior view; F: right posterior telopod, anterior view; G: right posterior telopod, posterior view. Abbreviations: Cx = coxa; O = operculum of vulva; Pre = prefemur; St-Pl = stigmatic plate; Syn-Cx = syncoxite. Scale bars = 1 mm.



**FIGURE 26.** *Sphaerobelum* sp. L10 (SMF); **A:** coxa of first left leg with first stigmatic plate; **B:** 9th left leg; **C:** coxa and prefemur of second leg with vulva; **D:** subanal plate. Abbreviations: **Cx** = coxa; **O** = operculum of vulva; **Pre** = prefemur; **St-Pl** = stigmatic plate. Scale bars = 1 mm.



**FIGURE 27.** *Sphaerobelum* sp. L07 (ZMUC); **A:** coxa of first left leg with first stigmatic plate; **B:** 9th left leg; **C:** coxa and prefemur of second leg with vulva; **D:** subanal plate. Abbreviations: **Cx** = coxa; **O** = operculum of vulva; **Pre** = prefemur; **St-Pl** = stigmatic plate. Scale bars = 1 mm.



**FIGURE 28.** *Sphaerobelum* sp. L04b (ZMUC); **A:** coxa of first left leg with first stigmatic plate; **B:** 9th left leg; **C:** coxa and prefemur of second leg with vulva; **D:** subanal plate. Abbreviations: **Cx** = coxa; **O** = operculum of vulva; **Pre** = prefemur; **St-Pl** = stigmatic plate. Scale bars = 1 mm.



## Acknowledgements

Many thanks to Christina L. Sagorny (University of Bonn) for her great work as a student assistant with the drawings and collecting characters from several of the species described here. Leif Moritz thankfully designed the maps. Scanning electron micrographs were thankfully prepared and taken by Rachel Werneck (ZFMK). Claudia Etzbauer (ZFMK) kindly provided lab support. Work on this article would not have been possible without the indispensable help of my assistant Thorsten Klug. Many thanks to the people who loaned out their specimens for a considerable amount of time: Henrik Enghoff (ZMUC), Peter Schwendinger (MHNG), as well as Peter Jäger and Julia Altmann (SMF). Many thanks also to the collectors, who found the here-described species as by-catch often under difficult conditions: Helmut Steiner, the above-mentioned Peter Jäger and Peter Schwendinger, as well as the other collectors. Sergei I. Golovatch together with an anonymous reviewer and the editor Paul Marek provided numerous comments which enhanced the quality of previous manuscript versions. Holly E. Wesener thankfully corrected the English.

## References

- Astrin, J.J. & Stüben, P.E. (2008) Phylogeny in cryptic weevils: molecules, morphology and new genera of western Palaearctic Cryptorhynchinae (Coleoptera: Curculionidae). *Invertebrate Systematics*, 22, 503–522.  
<https://doi.org/10.1071/IS07057>
- Attems, C. (1938) Die von Dr. C. Dawydoff in französisch Indochina gesammelten Myriopoden. *Mémoires du Muséum National d'Histoire Naturelle*, N. S. 6 (2), 187–353.
- Attems, C. (1953) Myriopoden von Indochina, Expedition von Dr. C. Dawydoff (1938–1939). *Mémoires du Muséum national d'histoire naturelle*, N. S., série A, 5 (3), 133–230.
- Car, C.A. & Harvey, M.S. (2014) The millipede genus *Antichiropus* (Diplopoda: Polydesmida: Paradoxosomatidae), part 2: species of the Great Western Woodlands region of Western Australia. *Records of the Western Australian Museum*, 29 (1), 20–77.  
[https://doi.org/10.18195/issn.0312-3162.29\(1\).2014.020-077](https://doi.org/10.18195/issn.0312-3162.29(1).2014.020-077)
- EIA (2011) Crossroads: The Illicit Timber Trade between Laos and Vietnam. Available from: <http://www.eia-international.org/wp-content/uploads/EIA-Crossroads-report-FINAL-low.pdf> (Accessed 28 Feb. 2019)
- Enghoff, H. (2005) The millipedes of Thailand (Diplopoda). *Steenstrupia*, 29 (1), 87–103.
- Enghoff, H., Golovatch, S., Short, M., Stoev, P. & Wesener, T. (2015) Diplopoda. In: Minelli, A. (Ed.), *Treatise on zoology—anatomy, taxonomy, biology. The Myriapoda*, 2 (16), 363–453.  
[https://doi.org/10.1163/9789004188273\\_017](https://doi.org/10.1163/9789004188273_017)
- Felsenstein, J. (1985) Confidence limits on phylogenies: An approach using the bootstrap. *Evolution*, 39, 783–791.
- Gan, J., Cerutti, P.O., Masiero, M., Pettenella, D., Andrighetto, N. & Dawson, T. (2016) *Quantifying Illegal Logging and Related Timber Trade* (No. IUFRO World Series no. 35). International Union of Forest Research Organizations (IUFRO), Vienna, Austria.
- Golovatch, S.I. (2016a) The millipede family Cryptodesmidae in Indochina (Diplopoda, Polydesmida). *ZooKeys*, 578, 33–43.  
<https://doi.org/10.3897/zookeys.578.7994>
- Golovatch, S.I. (2016b) On several new or poorly-known Oriental Paradoxosomatidae (Diplopoda: Polydesmida), XIX. *Arthropoda Selecta*, 25 (2), 131–152.
- Golovatch, S.I., Wesener, T., Mauriès, J.-P. & Semenyuk, I.I. (2012) On the identities of *Cryxus* Leach, 1814 and *Zephronia* Gray, 1832, the oldest generic names in the millipede order Sphaerotheriida (Diplopoda). *Arthropoda Selecta*, 21 (4), 273–294.
- Golovatch, S.I., Geoffroy, J.J., Mauriès, J.P. & VandenSpiegel, D. (2016a) Four new species of the millipede genus *Eutrichodesmus* Silvestri, 1910, from caves in Indochina (Diplopoda: Polydesmida: Haplodesmidae). *Arthropoda Selecta*, 25 (3), 247–256.
- Golovatch, S.I., VandenSpiegel, D. & Semenyuk, I.I. (2016b) On several new or poorly-known Oriental Paradoxosomatidae (Diplopoda: Polydesmida), XXI. *Arthropoda Selecta*, 25 (4), 335–354.
- Gray, G. (1832) The Myriapods (Myriapoda, Fab.). in Griffith E & Pidgeon E, The Class Insecta arranged by the Baron Cuvier, 1, 124–142, pl. 1–2.
- Likhitrakarn, N., Golovatch, S.I. & Panha, S. (2014a) A checklist of the millipedes (Diplopoda) of Laos. *Zootaxa*, 3754, 473–482.  
<https://doi.org/10.3897/zookeys.625.9846>
- Likhitrakarn, N., Golovatch, S.I. & Panha, S. (2014b) The millipede genus *Orthomorpha* Bollman, 1893 in Laos (Diplopoda, Polydesmida, Paradoxosomatidae), with descriptions of new species. *ZooKeys*, 374, 1–22.  
<https://doi.org/10.3897/zookeys.374.6711>

- Likhitrakarn, N., Golovatch, S.I. & Panha, S. (2014c) Review of the Southeast Asian millipede genus *Enghoffosoma* Golovatch, 1993 (Diplopoda, Polydesmida, Paradoxosomatidae), with descriptions of new species. *Zootaxa*, 3811 (4), 491–514.  
<https://doi.org/10.11646/zootaxa.3811.4.4>
- Likhitrakarn, N., Golovatch, S.I. & Panha, S. (2015a) Two new species of dragon millipedes, genus *Desmoxytes* Chamberlin, 1923, from Laos (Diplopoda: Polydesmida: Paradoxosomatidae), with redescrptions of all four species of Attems from Vietnam. *Zootaxa*, 3931 (4), 483–504.  
<https://doi.org/10.11646/zootaxa.3931.4.2>
- Likhitrakarn, N., Golovatch, S.I. & Panha, S. (2015b) Review of the millipede genus *Kronopolites* Attems, 1914 (Diplopoda, Polydesmida, Paradoxosomatidae), with the description of a new species from Laos. *ZooKeys*, 472, 27–41.  
<https://doi.org/10.3897/zookeys.472.9001>
- Likhitrakarn, N., Golovatch, S.I. & Panha, S. (2015c) A checklist of the millipedes (Diplopoda) of Cambodia. *Zootaxa*, 3973 (1), 175–84.  
<https://doi.org/10.11646/zootaxa.3973.1.7>
- Likhitrakarn, N., Golovatch, S.I. & Panha, S. (2016a) Review of the Southeast Asian millipede genus *Antheromorpha* Jeekel, 1968 (Diplopoda, Polydesmida, Paradoxosomatidae). *ZooKeys*, 571 (4), 21–57.  
<https://doi.org/10.3897/zookeys.571.7566>
- Likhitrakarn, N., Golovatch, S.I. & Panha, S. (2016b) The millipede genus *Tylopus* Jeekel, 1968 (Diplopoda, Polydesmida, Paradoxosomatidae), with a key and descriptions of eight new species from Indochina. *European Journal of Taxonomy*, 195, 1–47.  
<https://doi.org/10.5852/ejt.2016.195>
- Likhitrakarn, N., Golovatch, S.I., Inkhavilay, K., Sutcharit, C., Srisonchai, R. & Panha, S. (2017). Two new species of the millipede genus *Glyphiulus* Gervais, 1847 from Laos (Diplopoda, Spirostreptida, Cambalopsidae). *ZooKeys*, 722, 1–18.  
<https://doi.org/10.3897/zookeys.722.21192>
- Liu, W., Golovatch, S.I. & Wesener, T. (2017). Four new species of the millipede genus *Eutrichodesmus* Silvestri, 1910 from Laos, including two with reduced ozopores (Diplopoda, Polydesmida, Haplodesmidae). *ZooKeys*, 660, 43–65.  
<https://doi.org/10.3897/zookeys.660.11780>
- Moritz, L. & Wesener, T. (2017) Integrative description of two new species of Malagasy chirping giant pill-millipedes, genus *Sphaeromimus* (Diplopoda, Sphaerotheriida, Arthrosphaeridae). *European Journal of Taxonomy*, 381, 1–25.  
<https://doi.org/10.5852/ejt.2017.381>
- Nei, M. & Kumar, S. (2000) *Molecular evolution and phylogenetics*. Oxford university press, New York.
- Sagorny, C. & Wesener, T. (2017) Two new giant pill-millipede species of the genus *Zoosphaerium* endemic to the Bemanevika area in northern Madagascar (Diplopoda, Sphaerotheriida, Arthrosphaeridae). *Zootaxa*, 4263 (2), 273–294.  
<https://doi.org/10.11646/zootaxa.4263.2.4>
- Semenyuk, I., Golovatch, S.I. & Wesener, T. (2018) Four new species of giant pill-millipedes from Vietnam (Sphaerotheriida: Zephroniidae). *Zootaxa*, 4459 (3), 535–550.  
<https://doi.org/10.11646/zootaxa.4459.3.7>
- Smirnov, D. (2015) Assessment of Scope of illegal logging in Laos and associated trans-boundary timber trade. *WWF Unpublished report*, 1–106.
- Verhoeff, K.W. (1924) Results of Dr. E. Mjöberg's Swedish scientific expedition to Australia 1910-1913. 34. Myriapoda: Diplopoda. *Arkiv för Zoologi*, 16 (5), 1–142, pls.1–5.
- Wesener, T. (2009) Unexplored richness: Discovery of 31 new species of Giant Pill-Millipedes endemic to Madagascar, with a special emphasis on microendemism (Diplopoda, Sphaerotheriida). *Zootaxa*, 2097, 1–134.
- Wesener, T. (2015). Integrative redescription of a forgotten Italian pill millipede endemic to the Apuan Alps—*Glomeris apuana* Verhoeff, 1911 (Diplopoda, Glomerida, Glomeridae). *Zootaxa*, 4039 (2), 391–400.  
<https://doi.org/10.11646/zootaxa.4039.2.11>
- Wesener, T. (2016a) The Giant Pill-Millipedes, order Sphaerotheriida – An annotated species catalogue with morphological atlas and list of apomorphies (Arthropoda: Diplopoda). *Bonn Zoological Bulletin - Supplementum*, 63, 1–104
- Wesener, T. (2016b) Redescription and phylogenetic analysis of the type species of the giant pill-millipede genus *Sphaeropoeus* Brandt, 1833 (Diplopoda, Sphaerotheriida, Zephroniidae). *Zootaxa*, 4184 (1), 141–157.  
<http://doi.org/10.11646/zootaxa.4184.1.9>
- Wesener, T. (2018) An Integrative and Citizen Science based Approach to the Rediscovery and Redescription of the only known High-Altitude Endemic Pill Millipede, *Glomeris aurita* Koch (Diplopoda, Glomerida). *PeerJ*, 6:e5569.  
<https://doi.org/10.7717/peerj.5569>
- Wesener, T., Raupach, M.J. & Sierwald, P. (2010) The origins of the Giant Pill-Millipedes from Madagascar (Diplopoda: Sphaerotheriida: Arthrosphaeridae). *Molecular Phylogenetics and Evolution*, 57, 1184–1193.  
<https://doi.org/10.1016/j.ympev.2010.08.023>
- Wesener, T., Raupach, M.J. & Decker, P. (2011) Mountain Refugia Play A Role In Soil Arthropod Speciation On Madagascar. A case study of the endemic Giant Fire-Millipede genus *Aphistogoniulus* (Diplopoda, Spirobolida, Pachybolidae). *PLoS ONE*, 6 (12), 1–15.  
<https://doi.org/10.1371/journal.pone.0028035>

- Wesener, T. & Conrad, C. (2016) Local Hotspots of Endemism or Artifacts of Incorrect Taxonomy? The Status of Microendemic Pill Millipede Species of the Genus *Glomeris* in Northern Italy (Diplopoda, Glomerida). *PLoS ONE*, 11 (9), 1–22, e0162284.  
<https://doi.org/10.1371/journal.pone.0162284>
- Wesener, T. & Sierwald, P. (2005) The Giant Pill-Millipedes of Madagascar: Revision of the Genus *Sphaeromimus*, with a Review of the Morphological Terminology (Diplopoda, Sphaerotheriida, Sphaerotheriidae). *Proceedings of the California Academy of Sciences, Fourth Series*, 56 (29), 557–599.
- Wesener, T. & van den Spiegel, D. (2009) A first phylogenetic analysis of Giant Pill-Millipedes (Diplopoda: Sphaerotheriida), a new model Gondwanan taxon, with special emphasis on island gigantism. *Cladistics*, 25, 545–573.  
<https://doi.org/10.1111/j.1096-0031.2009.00267.x>
- Wongthamwanich, N., Panha, S., Sierwald, P., Wesener, T. & Thirakhupt, K. (2012) A new species of the giant pill-millipede genus *Sphaerobelum* Verhoeff, 1924 from northern Thailand, with an extensive description and molecular characters (Diplopoda: Sphaerotheriida: Zephroniidae). *Zootaxa*, 3220, 29–43
- WWF-Greater Mekong (2016) *Discovering the Greater Mekong*. Available from: [http://wwf.panda.org/what\\_we\\_do/where\\_we\\_work/greatermekong/discovering\\_the\\_greater\\_mekong/](http://wwf.panda.org/what_we_do/where_we_work/greatermekong/discovering_the_greater_mekong/) (Accessed 14 December 2016)